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Giant females vs dwarfish males of the genus *Stomaphis* Walker (Hemiptera: Aphididae) – an aphid example of the ongoing course to permanent parthenogenesis?

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Abstract

The aim of the study is a review of the sexual generation of European species of the aphid genus *Stomaphis* Walker. Oviparous females and males of *S.* (*Parastomaphis*) *longirostris* and *S.* (*Stomaphis*) *radicicola* are described and figured in detail. Poorly known sexuales of *S.* (*S.*) *bratislavensis*, *S.* (*S.*) *quercus*, *S.* (*S.*) *wojciechowskii*, *S.* (*P.*) *graffii*, and *S.* (*P.*) *juglandis* are redescribed and figured in detail. Biometric data for the oviparous females and males are reported and keys for the sexual generation of the studied species are provided. On the basis of the morphological characters of the sexuales, supported by biological data, the taxonomic status of the subgenus *Parastomaphis* Pašek, 1953 **stat. rev.** is discussed. Aberrations of male morphology are presented, with reference to the general phenomenon of male morphology deterioration in the genus *Stomaphis*. The discussion also refers to the mating behavior and general evolutionary factors influencing the development of male dwarfism in *Stomaphis*.

Key words

Copulation, dwarfism, lachnids, mating, sexual dimorphism.

1. Introduction

Approximately 5.000 species of Aphididae have been described so far (Favret 2014), all characterized by apomictic parthenogenesis (clonal or asexual reproduction) as either the main or exclusive mode of reproduction. Such a mode of reproduction is fairly rare in animals, but aphids are among those organisms which exploit it to the highest possible extent, i.e. as an adaptation that leads to a high population growth in a very short time and allows for a rapid niche exploitation in an altered habitat (Templeton 1982; Cuellar 1977; Clark 1973; Simon et al. 2002). However, in response to changes in environmental conditions, aphids alternate their reproductive mode from viviparous parthenogenesis in spring and summer (short nights) to oviparous sexual reproduction in autumn (long nights) (Dixon 1998). Under short-day conditions in autumn, sexual morphs (males and oviparous females) are produced parthenogenetically and morph determination (reproductive polyphenism) within mother aphids is regulated by a juvenile hormone (Ogawa & Miura 2014). The parthenogenesis switches to the sexual reproduction in almost all aphid lineages, and the typical life cycle (holocycle) consists of approximately 10–30 parthenogenetic generations, beginning with a viviparous female called the "fundatrix" or "stem mother," which hatches in spring from an overwintering egg, and which reproduces asexually, producing next generations

of viviparous, wingless "apterous" or winged "alate" females. The reproductive polyphenism, reflected by the occurrence of sexual morphs in response to the photoperiod, i.e. scotophase (the dark phase in a cycle of light and darkness, especially artifically induced) longer than 9–10 h (Hardie & Vaz Nunes 2001), is an adaptation to temperate climate conditions with severe winters – most aphid species overwinter at the egg stage (Dixon 1987). As the sexual generation occurs only for a short period of time, sexual morphs, and especially males of many aphid species, are either unknown or only incompletely described. Relatively little is known also about the copulatory behavior of aphids. This gap has been partly filled with detailed descriptions of male genitalia provided by Wieczorek et al. (2011, 2012) and single observations of mating behavior of selected species of Aphididae (Dagg & Scheurer 1998; Huang & Caillaud 2012).

A study of the genus *Stomaphis* Walker (Hemiptera: Aphididae: Lachninae) may provide insight into some interesting aspects of sexual reproduction in aphids. This Palaearctic genus comprises about 30 species associated both with deciduous trees and conifers (Blackman & Eastop 2014), and has many interesting features, making it a unique and very interesting model for studying some aspects of aphid biology. Viviparous females of *Stomaphis* are among the largest aphids, with body length reaching 8 mm, accompanied by an extremely long rostrum, which may twice exceed the length of the body. This long rostrum is an adaptation to the probing through deep bark crevices and the thick cork tissue of tree trunks, where these aphids feed. Their feeding locations stretch from the underground parts of the trunk base up to the height of several meters (Depa 2012, 2013). Despite their large body size, these aphids are rarely observed, because most species show a very cryptic mode of life (Depa et al. 2012). They have developed an obligate mutualistic relation with ants, predominantly those from the genus *Lasius* (Formicinae), and they cannot survive without their protection (Lorenz & Scheurer 1998). Thus, many species live hidden in ant chambers built under the bark or in bark crevices covered by soil. Additionally, in opposition to most aphid species, *Stomaphis* is characterized by a striking sexual dimorphism, i.e. oviparous females are large, with maximum body length about 7.70 mm, whereas males are very small (dwarfish), arostrate (without mouthparts and non-feeding), and thus are usually overlooked during field studies. As the sexual generation is scarcely recorded, many aspects of its biology, including mating behavior, have long remained unknown. Depa et al. (2014) reported atypical, ventro-ventral copulation position in those aphids; the life cycle of selected species was also studied by Goidanich (1958), Lorenz & Scheurer (1998), and Depa (2013). The sexuales of European *Stomaphis* species are poorly known, usually either described only briefly (Czylok & Blackman 1991; Petrović 1998; Depa et al. 2012) or unknown.

Here we present a review of the sexual generation of European *Stomaphis* species. On the basis of additional characters found in sexuales, supported by biological data, a redefinition of the subgenera *Stomaphis* and *Parastomaphis* proposed by Pašek (1953) is discussed. The known data on mating behavior, including the phenomenon of cryptic sex during atypical copulation, is summarized. The question whether male dwarfism in aphids leads to permanent parthenogenesis is discussed.

2. Materials and methods

Regular field studies of the sexual generation of the genus *Stomaphis* were carried out in southern Poland in the years 2010–2013 (from mid-August to mid-November). Adult males and oviparous females of four species were observed and collected: *S.* (*S.*) *quercus*, *S.* (*S.*) *wojciechowskii*, *S.* (*P.*) *graffii* and *S.* (*P.*) *longirostris*, as well as nymphs of males of two species: *S.* (*S.*) *quercus* and *S.* (*P.*) *graffii*. The activity of attending ants was also noted. Additional material of the above mentioned species and specimens of *S.* (*S.*) *bratislavensis*, *S.* (*S.*) *radicicola* and *S.* (*P.*) *juglandis* were borrowed from the following scientific collections (preceded by acronyms used in this paper): MNHN = Muséum national d'Histoire naturelle, Paris, France; UŚ = Department of Zoology, University of Silesia, Katowice, Poland; in these institutions the examined slides are deposited.

We examined 143 mounted specimens of known European sexuales of *Stomaphis*. From 1 to 10 specimens of both oviparous females and males of each species were measured. The slides were examined using a Nikon Ni-U light microscope and photographed with a Nikon DS-Fi2 camera. Field photographs were taken with a Sony SLT a37 digital camera, using Sigma 50 mm macro lenses with external rings. Drawings were made with a camera lucida. We followed the protocol described by Kanturski & Wieczorek (2012) for whole mount preparations of specimens. The terminology of the male genitalia follows Wieczorek et al. (2012). SEM photographs were taken with a Philips XL 30 ESEM/TMP; the specimens were examined in low vacuum conditions, p = 0.3 torr by SE and BSE detectors (Scanning Microscopy Laboratory, Faculty for Earth Sciences, University of Silesia, Poland).

Measurements of studied specimens are given in millimeters. Ratios are provided in the descriptions using the following abbreviations: **BL** = body length (from anterior border of the head to the end of cauda); **HW** = greatest head width across compound eyes; **ANT I–VI** = antennomeres I–VI (length ratios between antennomeres are simply given as e.g. 'VI/III'); **VIa** = base of antennomere VI; **VIb** = processus terminalis of antennomere VI; **ant. III BD** = basal articular diameter of antennomere III; **sec. rhin.** = secondary rhinaria; **prim. rhin.** = primary rhinaria; **acc. rhin.** = accessory rhinaria; **ARS** = apical rostral segment (IV+V); **MT II** = second segment of middle tarsus; **HT I** = first segment of hind tarsus; **HT II** = second segment of hind tarsus; **abd. terg. I–VIII** = abdominal tergites I–VIII; **abd. stern. I–VIII** = abdominal sternites I–VIII.

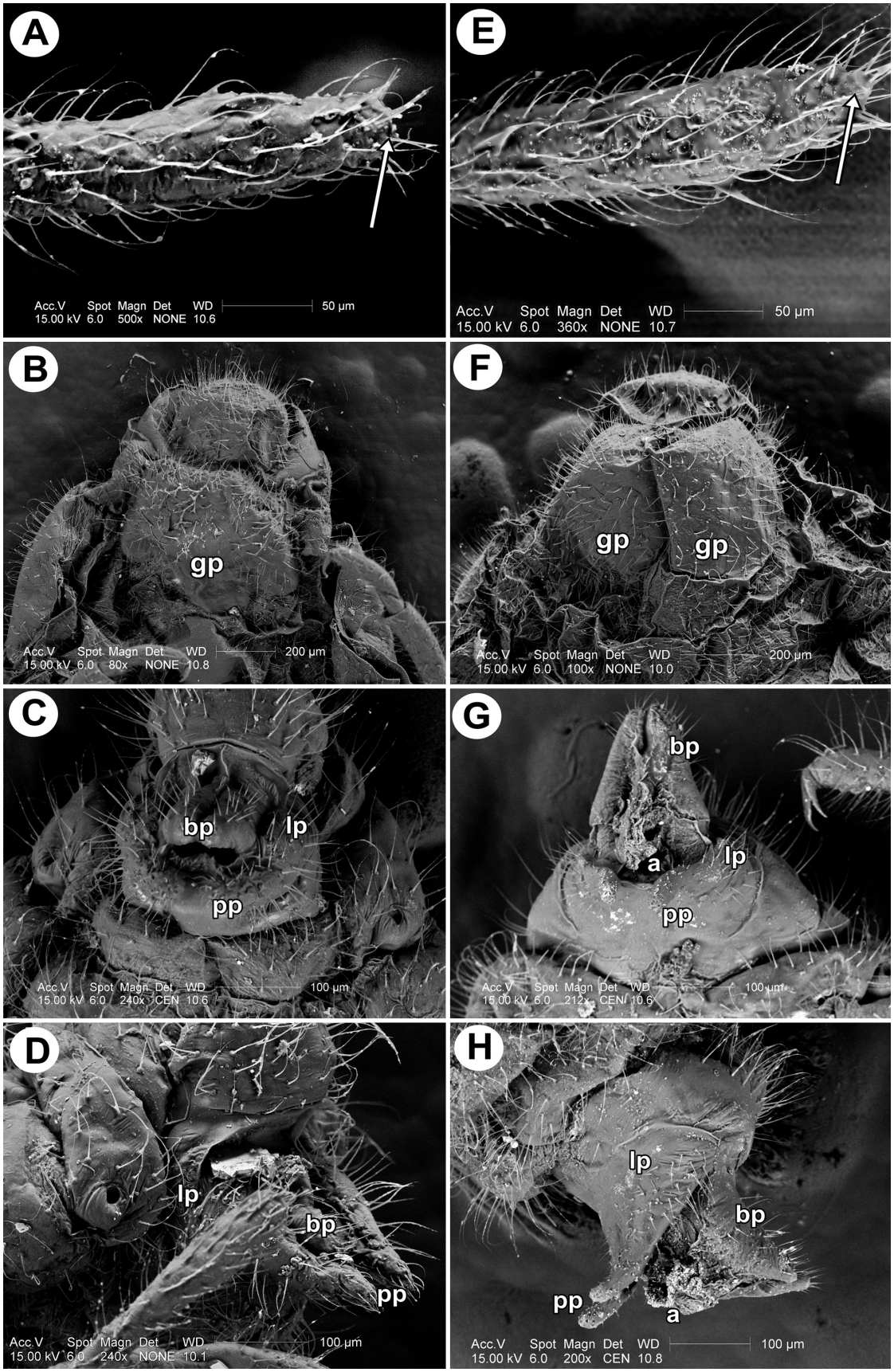

Fig. 1. Morphological features of the sexual generation distinguishing subgenera *Stomaphis* and *Parastomaphis*. *S.* (*S.*) *quercus*: oviparous female, **A**: ANT VIb without nodulose bases of setae (arrow), **B**: genital plate not divided into separate plates; male, **C**,**D**: external genitalia. *S.* (*P.*) *graffi*: oviparous female, **E**: ANT VIb with nodulose bases of setae (arrow), **F**: genital plate divided into distinct two separate plates; male, **G**,**H**: external genitalia. — ***Abbreviations***: **gp** = genital plate, **a** = aedeagus, **lp** = lobate part of parameres, **pp** = projections of parameres, **bp** = basal part of phallus.

3. Results

3.1. Systematics

Shared characters of European *Stomaphis*

Oviparous females. Body large, oval, covered with dense pubescence and fine, pointed setae. Head short, wide, with well-defined median suture. Compound eyes with weakly developed triommatidium. Antennae 6-segmented, covered with dense pubescence. Length of antennal setae slightly less than diameter of segments. Apical setae on ANT VIb without nodulose bases in *Stomaphis* (Fig. 1A) and on a nodulose base in *Parastomaphis* (Fig. 1E). Primary rhinaria on ANT V and VI slightly oval with delicate sclerotic rim. Rostrum very long. Rostral segment II provided with many scleroites around setal bases. ARS blunt with numerous setae. Pronotum pigmented, sclerotized. Mesosternal and metasternal processes weakly developed. Hind tibiae not swollen, without pseudosensoria. Siphunculi porous. Genital plate wide, wider than in apterous vivipara, but less sclerotized, with finely defined distal edge, covered with numerous short setae; not divided in *Stomaphis* (Fig. 1B), consisting of two separate sclerotic plates in *Parastomaphis* (Fig. 1F). Cauda broadly rounded, not well developed, covered with long sharp setae. A row of sclerotic patches on the abdominal sternites (ventral plates) are present in *Stomaphis* but absent in *Parastomaphis*.

Males. Wingless, dwarfish. Body elongate, oval, slightly egg-shaped. Head short, wide, with a weakly defined median suture. Triommatidium present. Antennae 6-segmented. Apical setae on ANT VI without nodulose bases in *Stomaphis* and with nodulose bases in *Parastomaphis*. Antennomeres densely covered with erect setae, in *Stomaphis* equal to diameter of segment bases, in *Parastomaphis* slightly less than diameter of segment bases. Primary rhinaria on ANT V and VI without sclerotic rosette, slightly oval. Pronotum and mesonotum sclerotized. Mesothoracic and metathoracic furcae weakly developed. Metanotum with hardly developed spinal and marginal sclerotisations. Thoracic and abdominal spiracles placed on small sclerites, slightly darker than sclerotized main parts of tergites. Rostrum absent, only reduced clypeus present. Legs covered with many erect setae, their length in *Stomaphis* equal to and in *Parastomaphis* less than diameter of tibia. Siphunculi absent. Cauda broadly rounded, not well developed, covered with long, pointed setae. Abdomen with transverse rows of many setae placed on small and weakly sclerotized plates along all abdominal tergites. Genitalia consisting of phallus and parameres. The phallus is composed of a sclerotized basal part with its articulation, i.e. proximal and distal part of sclerotized arms, and a membranous apical part, the aedeagus. Parameres are strongly modified, located above the basal part of the phallus, divided into pair of fused lobate proximal parts extended into variously shaped projections (Figs. 1C,D,G,H, 9A–F). In *Stomaphis* projections of parameres are short and wide, the basal part of the phallus is club-shaped and short (Figs. 1C,D, 9A–C), whereas in *Parastomaphis* projections of parameres are long and the basal part of the phallus is lanceolate and elongate (Figs. 1G,H, 9D–F). In *Stomaphis* both parameres and the basal part of the phallus are entirely covered with numerous, long setae (Fig. 1D) whereas in *Parastomaphis* only the parameres and the apices of the basal part of the phallus are setose (Fig. 1H).

Key to European *Stomaphis*: oviparous females

1 Ventral plates present (Figs. 2, 3, 4, 5) **2**
1' Ventral plates absent (Figs. 6, 7, 8) **5**
2 Spinal plates on abdominal tergites I–VI present (Figs. 3, 5) **3**
2' Spinal plates on abdominal tergites I–VI absent (Figs. 2, 4) **4**
3 HT II/MT II 1.29–1.41, ANT VI/ANT III 0.69–0.78; in life dark green to blackish brown, shining ..... ***Stomaphis* (*S.*) *quercus* (L.)**
3' HT II/MT II 1.26–1.28, ANT VI/ ANT III 0.79–0.80; in life fuscous, dull, slightly wax powdered ..... ***Stomaphis* (*S.*) *wojciechowskii* Depa**
4 First ventral plate crescent-shaped (Fig. 4); HT II/MT II 1.30–1.37 ..... ***Stomaphis* (*S.*) *radicicola* Hille Ris Lambers**
4' All ventral plates narrow, elongate (Fig. 2); HT II/MT II 1.60–1.70 ... ***Stomaphis* (*S.*) *bratislavensis* Czylok & Blackman**
5 HW/AL > 0.55; ARS/ANT. III > 0.80; ARS/HT II < 1.55 ..... **6**
5' HW/AL 0.50–0.52; ARS/ANT. III 0.70–0.77; ARS/HT II 1.60 ..... ***Stomaphis* (*P.*) *juglandis* Petrović**
6 Abd. terg. VII at most with small, separate spinal scleroites; middle trochanter 0.10–0.16 mm long; ANT III+IV+V+VI/ARS 2.70–3.03; on *Acer* spp. ..... ***Stomaphis* (*P.*) *graffii* Cholodkovsky**
6' Abd. terg. VII at least with single spinal scleroites, usually with small sclerotic plates; middle trochanter 0.17–0.18 mm long; ANT III+IV+V+VI/ARS 2.49–2.69; on Salicaceae ..... ***Stomaphis* (*P.*) *longirostris* (Fabricius)**

Key to European *Stomaphis*: males

(male of *S. bratislavensis* not included)

1 Apical setae on VIb without nodulose bases (Fig. 1A); length of setae on antennae equal to diameter of segment bases. Projections of parameres short and wide. Basal part of phallus club-shaped, short (Figs. 9A,B,C) **2**
1' Apical setae on VIb with nodulose bases (Fig. 1E); length of setae on antennae slightly less than diameter of segment bases. Projections of parameres long. Basal part of phallus lanceolate, elongate (Figs. 9D, E,F) **4**
2 HT II/ANT VI < 1.0 ..... **3**

Table 1. Measurements of main characters of oviparous females of the European species of the genus *Stomaphis.*

Character	Oviparous females						
	Stomaphis* (*Stomaphis*) *bratislavensis n = 2	***Stomaphis* (*Stomaphis*) *quercus*** n = 10	***Stomaphis* (*Stomaphis*) *radicicola*** n = 3	***Stomaphis* (*Stomaphis*) *wojciechowskii*** n = 5	***Stomaphis* (*Parastomaphis*) *graffii*** n = 10	***Stomaphis* (*Parastomaphis*) *juglandis*** n = 1	***Stomaphis* (*Parastomaphis*) *longirostris*** n = 10
Length of body	5.00 – 5.12	6.15 – 7.37	5.27 – 5.70	5.67 – 6.39	5.90 – 6.97	7.27	6.20 – 7.70
Maximum width	3.00 – 3.22	2.27 – 4.07	2.85 – 3.20	2.77 – 3.47	2.95 – 3.72	3.90	3.45 – 4.30
Head width	1.19 – 1.22	1.27 – 1.50	1.10 – 1.30	1.30 – 1.40	1.27 – 1.42	1.32	1.27 – 1.47
Antennae length	2.76 – 2.78	2.27 – 2.57	1.81 – 2.26	2.08 – 2.14	1.83 – 2.24	2.55 – 2.62	1.99 – 2.25
Antennomere III	0.72 – 0.75	0.68 – 0.80	0.59 – 0.63	0.60 – 0.63	0.61 – 0.75	0.93 – 0.94	0.60 – 0.74
Antennomere IV	0.44 – 0.45	0.36 – 0.43	0.32 – 0.35	0.30 – 0.35	0.31 – 0.38	0.40 – 0.41	0.31 – 0.40
Antennomere V	0.60	0.36 – 0.41	0.36 – 0.42	0.32 – 0.36	0.36 – 0.46	0.50 – 0.52	0.37 – 0.41
Antennomere VI	0.64 – 0.65	0.52 – 0.59	0.48 – 0.54	0.47 – 0.51	0.31 – 0.36	0.39 – 0.40	0.31 – 0.36
Antennomere VIa	0.57 – 0.58	0.43 – 0.50	0.41 – 0.44	0.38 – 0.41	0.25 – 0.29	0.32 – 0.33	0.25 – 0.30
Antennomere VIb	0.068 – 0.070	0.08 – 0.09	0.07 – 0.09	0.07 – 0.10	0.06 – 0.08	0.06 – 0.07	0.04 – 0.07
Middle femora length	0.99 – 1.00	0.90 – 1.12	0.94 – 0.98	0.87 – 0.90	0.90 – 1.10	0.47	0.87 – 1.05
Middle tibiae length	1.37	1.27 – 1.65	1.27 – 1.32	1.12 – 1.27	1.25 – 1.40	1.35	1.00 – 1.40
Hind femora length	1.50	1.30 – 1.52	1.27 – 1.37	1.25 – 1.32	1.27 – 1.42	1.42 – 1.47	1.30 – 1.47
Hind tibiae length	2.55 – 2.60	2.05 – 2.60	2.02 – 2.17	1.90 – 2.15	1.87 – 2.12	2.17 – 2.25	1.67 – 2.10
HT I length	0.14 – 0.15	0.12 – 0.14	0.14 – 0.15	0.12	0.14 – 0.17	0.15 – 0.16	0.15 – 0.17
HT II length	0.52 – 0.53	0.36 – 0.41	0.39 – 0.41	0.35 – 0.36	0.41 – 0.47	0.45	0.44 – 0.50
ARS	0.72 – 0.74	0.65 – 0.77	0.55 – 0.56	0.63 – 0.65	0.60 – 0.65	0.72	0.63 – 0.71
Siphuncular sclerite length	0.88 – 0.91	0.60 – 0.80	0.80 – 0.85	0.59 – 0.65	0.53 – 0.74	0.80 – 0.88	0.52 – 0.75
Siphuncular sclerite width	0.35	0.35 – 0.47	0.44 – 0.50	0.34 – 0.40	0.42 – 0.55	0.62 – 0.63	0.37 – 0.50
Genital plate length	0.45	0.47 – 0.52	0.60 – 0.62	0.40 – 0.47	0.50 – 0.65	0.60	0.50 – 0.58
Genital plate width	1.05	0.90 – 1.09	0.97 – 1.05	0.80 – 1.00	0.90 – 1.15	1.40	0.96 – 1.22

Table 2. Measurements of main characters of males of the European species of the genus *Stomaphis.*

Character	Males					
	Stomaphis* (*Stomaphis*) *quercus n=10	***Stomaphis* (*Stomaphis*) *radicicola*** n=3	***Stomaphis* (*Stomaphis*) *wojciechowskii*** n=8	***Stomaphis* (*Parastomaphis*) *graffii*** n=10	***Stomaphis* (*Parastomaphis*) *juglandis*** n=1	***Stomaphis* (*Parastomaphis*) *longirostris*** n=10
Length of body	2.50–2.85	2.37–2.52	2.12–2.45	2.06–3.05	3.27	2.25–3.22
Maximum width	1.02–1.32	1.05–1.10	1.00–1.12	1.12–1.32	1.37	1.10–1.40
Head width	0.60–0.65	0.61–0.65	0.52–0.53	0.57–0.65	0.74	0.58–0.65
Antennae length	1.46–1.70	1.55–1.67	1.19–1.27	1.29–1.76	1.78	1.35–1.64
Antennomere III	0.37–0.45	0.34–0.39	0.31–0.37	0.41–0.50	0.67	0.39–0.53
Antennomere IV	0.22–0.29	0.23–0.25	0.19–0.22	0.12–0.20	0.25	0.12–0.22
Antennomere V	0.24–0.32	0.26–0.34	0.20–0.26	0.27–0.37	0.37	0.29–0.34
Antennomere VI	0.29–0.40	0.32–0.37	0.27–0.32	0.26–0.32	0.24	0.22–0.30
Antennomere VIa	0.24–0.30	0.26–0.31	0.21–0.26	0.21–0.25	0.20	0.17–0.25
Antennomere VIb	0.05–0.10	0.06–0.08	0.04–0.06	0.05–0.07	0.04	0.03–0.06
Middle femora length	0.51–0.62	0.55–0.60	0.46–0.50	0.55–0.64	0.65	0.52–0.69
Middle tibiae length	0.70–0.80	0.78–0.83	0.60–0.68	0.74–0.86	0.88	0.69–0.87
MT II length	0.22–0.25	0.24–0.25	0.20–0.23	0.25–0.28	0.25	0.25–0.29
Hind femora length	0.62–0.72	0.64–0.68	0.54–0.60	0.72–0.83	0.90	0.67–0.84
Hind tibiae length	0.95–1.10	0.98–1.05	0.80–0.87	1.00–1.15	1.25	0.90–1.15
HT I length	0.08–0.09	0.08–0.09	0.07–0.08	0.08–0.12	0.11	0.10–0.11
HT II length	0.24–0.28	0.27–0.28	0.23–0.25	0.30–0.38	0.35	0.29–0.36

2' HT II/ANT VI 1.05 – 1.22
..... ***Stomaphis* (*S.*) *radicicola* Hille Ris Lambers**

3 HW 0.60 – 0.65 mm; AL 1.46 – 1.70 mm; ANT IV 0.22 – 0.29 mm ..... ***Stomaphis* (*S.*) *quercus* (L.)**

3' HW 0.52 – 0.53 mm; AL 1.19 – 1.27 mm; ANT IV 0.19 – 0.22 mm
..... ***Stomaphis* (*S.*) *wojciechowskii* Depa**

4 ANT III < 0.55 mm; ANT III/ANT VI > 0.45; HTII/ANT III > 0.60 ..... **5**

4' ANT III > 0.60 mm; ANT III/ANT VI < 0.40; HTII/ANT III < 0.60
..... ***Stomaphis* (*P.*) *juglandis* Petrović**

5 Projections of parameres covered by few short setae on apices (Figs. 1G,H, 9D)
..... ***Stomaphis* (*P.*) *graffii* Cholodkovsky**

5' Projections of parameres covered by numerous setae (Fig. 9F)
..... ***Stomaphis* (*P.*) *longirostris* (Fabricius)**

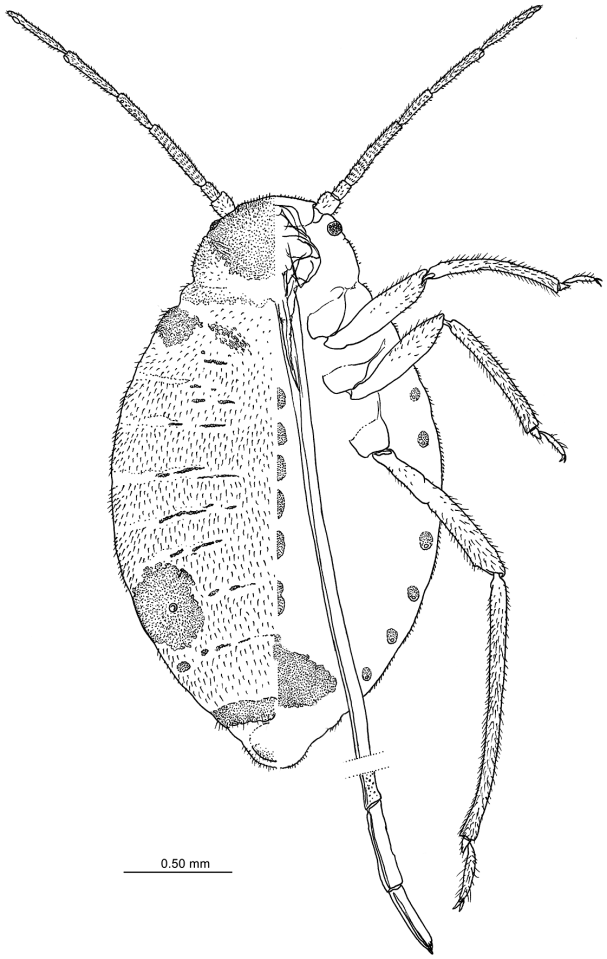

Fig. 2. *Stomaphis* (*S.*) *bratislavensis*. Oviparous female.

Genus *Stomaphis* Walker, 1890

Macrhynchus Haupt, 1913
Neostomaphis Takahashi, 1960
Rhynchocles Altum, 1882
Subgenus *Stomaphis* Walker, 1890

Stomaphis (*Stomaphis*) *bratislavensis* Czylok & Blackman, 1991

Redescription, oviparous female (Fig. 2; Table 1). ***Colour*** of live specimens: fuscous, dull, slightly wax powdered (Czylok & Blackman 1991). Mounted specimens: body brownish, head brown, antennae uniformly brown. Legs light brown, hind femora light brown with darker knee area, tibiae light brown with external edges darker, tarsi light brown. Siphuncular sclerites, ventral plates, genital plate and cauda brown. ***Antennae*** 0.45–0.52 × BL and 1.94–2.26 × HW. ANT VI equal to V, VIb 0.13–0.12 × VIa; other antennal ratios: VI/III 0.87–0.89, V/III 0.80–0.83, IV/III 0.59–0.62. VIb without apical setae and with 20–30 subapical setae. ANT III with 2–7 sec. rhin., segm. IV with 7 sec. rhin., without sclerotic rosette. Prim. rhin. on ANT VI oval-shaped, surrounded by 5–6 small acc. rhin., diffused along distal half of VIa. ***Rostrum*** when extended 2.09 × BL. ARS 0.97–1.01 × ANT III and 1.38–1.40 × HT II. Labrum on microscopic slides missing. ***Sclerotization***: Mesonotum and metanotum with marginal sclerites. Abd. terg. only with sclerotic band on abd. terg. VII; sclerotic cones around siphuncular pore and sclerites around spiracles and also some minute scleroites around setae-bases on posterior tergites. Abd. stern. with 6 glabrous, weakly sclerotized patches in medial longitudinal row, ornamented with spinulose miscrosculpture. Siphuncular sclerite large with proximal part subdivided into a few smaller scleroites.
Male (after Czylok & Blackman 1991; from one specimen). Body in life light brown in colour. Antennae 2.6 × as long as head with across eyes. Length of antennomere in mm: III 0.51, IV 0.24, V 0.36, VI 0.41. Antennae lack secondary rhinaria. Compound eyes with 16 facets and a triommatidium. Abdomen weakly sclerotized. Claspers (= parameres) deeply incised, the arms covered with bristly hairs and the base with long hairs. Basal sheath of penis (= basal part of phallus) with short bristly pubescence. Body length 2.86 mm, maximum width 1.35 mm.

Material examined. ***Paratypes***: 1♀ CSR, distr. Bratyslava, Šur, 5.x.1988, Czylok leg., coll. UŚ no. 10/88/03; 1♀ CSR, distr. Bratyslava, Šur, 5.x.1988, Czylok leg., coll. UŚ no. 10/88/04.

Stomaphis (*Stomaphis*) *quercus* (Linnaeus, 1758)

Aphis fusca (Geoffroy, 1762)
Phylloxera longirostris Boyer de Fonscolombe, 1841
Rhynchocles longirostris Altum, 1882
Stomaphis macrorhyncha Cholodkovsky, 1894
Macrhynchus pini Haupt, 1913
Stomaphis betulae Mamontova, 1969

Redescription, oviparous female (Figs. 1A,B, 3A, 15C,D; Table 1). ***Colour*** of live specimens: dark green to blackish brown, shining. Mounted specimens: body yellowish with spinal and ventral plates and marginal sclerites brown. Head brown, antennae dusky with slightly darker apices of segm. III–VI. Legs light brown, hind femora light brown with darker knee area, tibiae light brown with external edges darker, tarsi brown. Siphuncular sclerites, genital plate and cauda brown. ***Antennae*** 0.32–0.42 × BL and 1.53–1.98 × HW. ANT VI longer than V, VIb 0.19–0.24 × VIa; other antennal ratios: VI/III 0.69–0.79, V/III 0.49–0.59, IV/III 0.51–0.59. VIb with 2 apical and 14–18 subapical setae. ANT III with 0–6 sec. rhin., segm. IV with 0–6 sec. rhin., without sclerotic rosette, primary rhinaria on ANT VI oval in shape, surrounded by 1–3 small acc. rhin. ***Rostrum*** when extended 1.65–2.27 × BL. ARS 0.88–1.08 × ANT III and 1.67–1.88 × HT II. Labrum covered with 20–30 setae along its entire length. ***Sclerotization***: Mesonotum and

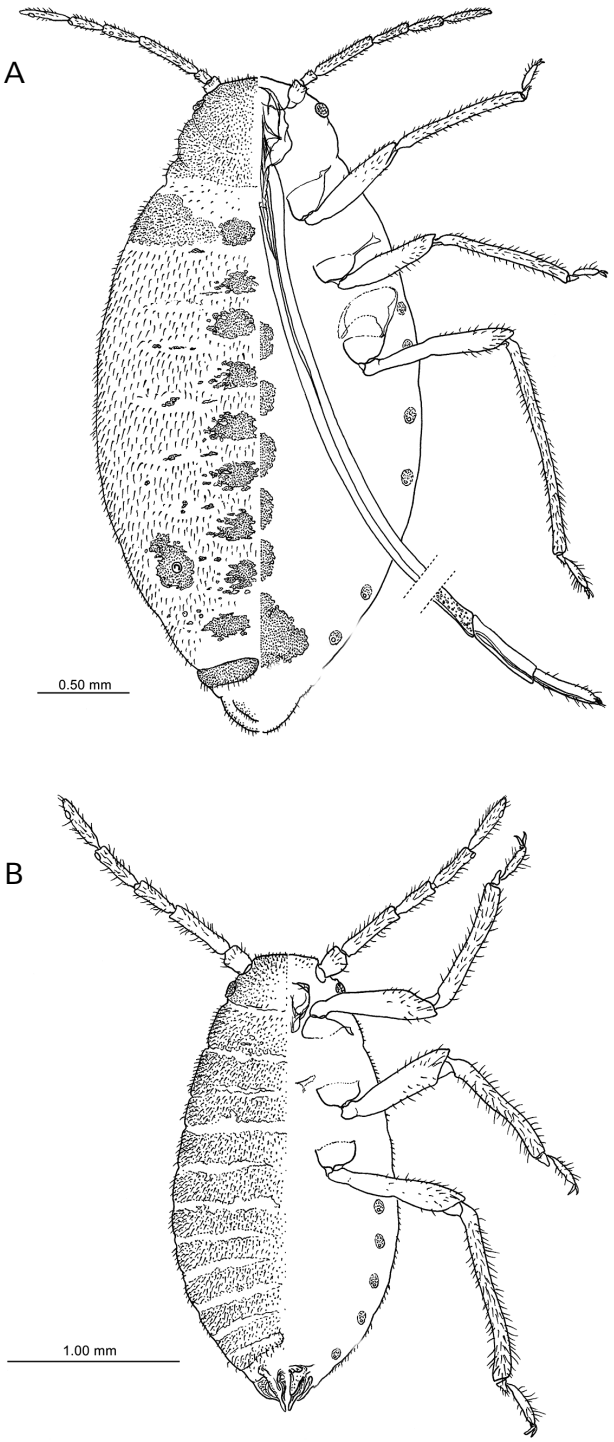

Fig. 3. *Stomaphis* (*S.*) *quercus*. **A**: Oviparous female. **B**: Male.

metanotum with spinal and marginal sclerites. Abd. terg. with row of paired spinal sclerites on each abd. segm., sclerotic cones around siphuncular pore and sclerites around spiracles and also some minute scleroites around setae-bases on posterior tergites. Abd. stern. with 6 glabrous, intensely sclerotized and dark pigmented patches in medial longitudinal row, ornamented with finely spinulose miscrosculpture. Siphuncular sclerite with proximal part subdivided into many smaller scleroites.

Redescription, male (Figs. 1C,D, 3B, 9A, 10B,E, 15C,D; Table 2). ***Colour*** of live specimens: dark green. Mounted specimens: body brownish, head and antennae dark brown. Hind legs light brown, hind femora yellowish-brown with apices slightly darker, knees brown, tibiae yellowish-brown with dark apices, tarsi brown. Cauda and genitalia brown. Compound eyes each with 10–22 facets. ***Antennae*** 0.54–0.64 × BL and 2.36–2.73 × HW. VIb 0.19–0.33 × VIa; other antennal ratios: VI/III 0.70–1.03, V/III 0.60–0.82, IV/III 0.54–0.71. VIb with 2–3 apical and 16–23 subapical setae. Prim. rhin. on ANT VI surrounded by 1–5 small acc. rhin. ***Sclerotization***: Dorsum sclerotized, with weakly developed sclerotic cross bars and scleroites at bases of setae. ***Genitalia*** (Figs. 1C,D, 9A) projections of parameres very short and wide, covered with numerous setae shorter than on pair of lobate parts. Basal part of phallus rather short, club-shaped, dusky, sclerotized on inner margin, with numerous long setae. Sclerotized arms dark pigmented, with proximal part short and robust and distal part elongated and smooth.

Material examined. 7♂ juv. POLAND, Piekary Śląskie Lipka, 13.viii.2011, *Betula verrucosa*, Depa leg., coll. UŚ no. S 219 D; 4♂, 5♀ SLOVENIA, Dobrova, 30.ix.2011, *Quercus robur*, Depa leg., coll. UŚ no. S 114; 4♂, 9♀ SLOVAKIA, Svaty Jur, 3.x.2011, *Q. robur*, Depa leg., coll. UŚ no. S 131A, B; 7♂, 5♀ POLAND, Jarosław, 25.x.2010, *Q. robur*, Depa leg., coll. UŚ no. S 212 A, B, C, D; 3♂, 7♀ POLAND, Piekary Śląskie Lipka, 9.x.2010, *B. verrucosa*, Depa leg., coll. UŚ no. S 212 A, S 212 E.

Stomaphis (*Stomaphis*) *radicicola* Hille Ris Lambers, 1947

Redescription, oviparous female (Fig. 4A; Table 1). ***Colour*** of live specimens: fuscous, weakly wax powdered. Mounted specimens: body brownish with ventral plates and marginal sclerites brown. Head brown, antennae uniformly brown. Legs light brown, hind femora with darker knee area, tibiae light brown with external edges darker, tarsi light brown. Siphuncular sclerites, genital plate and cauda brown. ***Antennae*** 0.39–0.41 × BL and 1.69–2.06 × HW. ANT VI longer than V, VIb 0.18–0.22 × VIa; other antennal ratios: VI/III 0.81–0.87, V/III 0.60–0.67, IV/III 0.52–0.57. VIb with 3 apical and 15–18 subapical setae. ANT III with 0–2 sec. rhin., segm. IV with 1–5 sec. rhin. Prim. rhin. on ANT VI oval in shape, surrounded by 1–2 small acc. rhin. ***Rostrum*** when extended 1.17–1.31 × BL. ARS 0.87–0.92 × ANT III and 1.34–1.43 × HT II. Labrum covered with about 25–35 setae along its entire length. ***Sclerotization***: Mesonotum with spinal and marginal sclerites, metanotum with marginal sclerites. Abd. terg. VII with pair of small spinal sclerites. Siphuncular pore surrounded by single, big sclerotic plate. Abd. stern. with 6 glabrous, intensely sclerotized and dark pigmented patches (first one is smaller and crescent-like) in medial longitudinal row, ornamented with finely spinulose miscrosculpture.

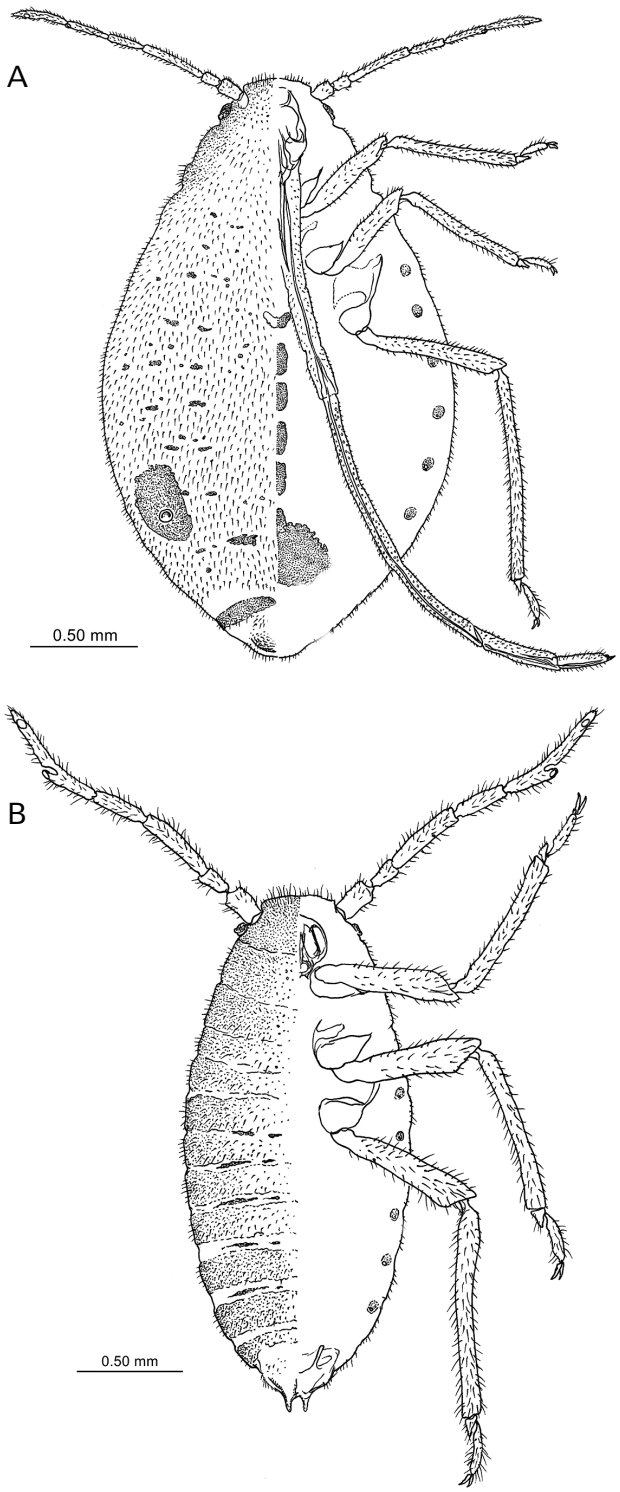

Fig. 4. *Stomaphis* (*S.*) *radicicola*. **A**: Oviparous female. **B**: Male.

Description, male (Figs. 4B, 9B, 11E; Table 2). ***Colour*** of live specimens: unknown. Mounted specimens: body light brown, with head, legs and antennae darker, genitalia dark brown. Compound eyes each with 6–11 facets. ***Antennae*** 0.62–0.68 × BL and 2.40–2.74 × HW. ANT V and VI (Fig. 11E) not fully separated in some specimens. VIb 0.21–0.30 × VIa; other antennal ratios: VI/III 0.82–1.05, V/III 0.69–0.94, IV/III 0.58–0.72. VIb with 3–5 apical and 12–16 subapical setae. Prim. rhin. on ANT VI surrounded by 1–4 small acc. rhin. ***Sclerotization***: Pronotum and mesonotum weakly sclerotised. Intersegmental muscle sclerites well developed and clearly visible. Thoracic and abdominal spiracles placed on small sclerites, slightly darker than sclerotized plates on tergites. ***Genitalia*** (Fig. 9B) in general appearance similar to *S.* (*S.*) *quercus* with projections of parameres smooth and much longer with less numerous setae on apices. Sclerotized arm robust, of similar length to proximal and distal part.

Material examined. 3♂, 2♀ FRANCE, St. Medar (Gironde), 13.xi.1956, *Alnus glutinosa*, Remaudière leg., coll. MNHN no.17568, 17569, 17570; 1♀ SLOVAKIA, Svaty Jur, 3.x.2011, *A. glutinosa*, Depa leg., coll. UŠ no. S 133a.

Stomaphis (*Stomaphis*) *wojciechowskii* Depa, 2012

Redescription, oviparous female (Figs. 5A, 15E; Table 1). ***Colour*** of live specimens: fuscous, dull, slightly wax powdered. Mounted specimens: body brownish with spinal and ventral plates and marginal sclerites brown. Head brown, antennae uniformly dusky. Legs light brown, hind femora light brown with darker knee area, tibiae light brown with external edges darker, tarsi brown. Siphuncular sclerites, genital plate and cauda brown. ***Antennae*** 0.33–0.37 × BL and 1.49–1.65 × HW. ANT VI longer than V, VIb 0.19–0.25 × VIa; other antennal ratios: VI/III 0.79–0.81, V/III 0.54–0.57, IV/III 0.48–0.58, VIb with 1–2 apical and 19–28 subapical setae. ANT III with 0–1 sec. rhin., segm. IV with 4–5 sec. rhin., without sclerotic rosette. Prim. rhin. on ANT VI oval in shape, surrounded by 4–6 small acc. rhin., diffused along the distal half of VIa. ***Rostrum*** when extended 1.90–2.30 × BL. ARS 1.03–1.05 × ANT III and 1.77–1.81 × HT II. Labrum covered with 15–25 setae along its entire length. ***Sclerotization***: Mesonotum and metanotum with spinal and marginal sclerites. Abd. terg. with row of paired, spinal sclerites on each abd. segm., which are always divided into many smaller scleroites, sclerotic cones around siphuncular pore and sclerites around spiracles and also some minute scleroites around setae-bases on posterior tergites. Abd. stern. with 6 glabrous, intensely sclerotized and dark pigmented patches in medial longitudinal row, ornamented with finely spinulose miscrosculpture. Siphuncular sclerite with proximal part subdivided into many smaller scleroites.

Redescription, male (Figs. 5B, 9C, 12C; Table 2). ***Colour*** of live specimens: olive green. Mounted specimens: body brownish, head and antennae light brown. Hind legs light brown, hind femora yellowish-brown with apices slightly darker, knees brown, tibiae yellowish-brown with dark apices, tarsi brown. Cauda and genitalia brown. Compound eyes each with 11–14 facets. ***Antennae*** 0.52–0.60 × BL and 2.30–2.45 × HW. VIb 0.21–0.26 × VIa; other antennal ratios: VI/III 0.82–

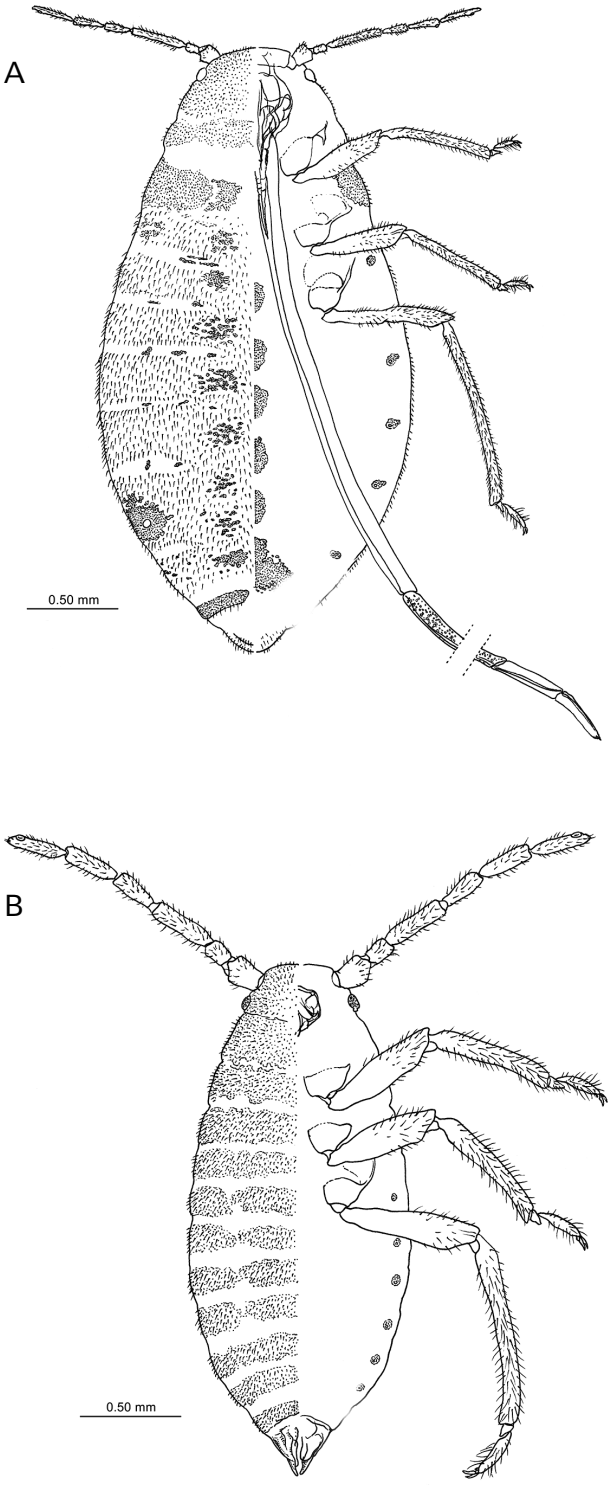

Fig. 5. *Stomaphis* (*S.*) *wojciechowskii*. **A**: Oviparous female. **B**: Male.

0.86, V/III 0.63–0.70, IV/III 0.54–0.60. VIb with 1–2 apical and 16–22 subapical setae. Prim. rhin. on ANT VI surrounded by 4–5 small acc. rhin. ***Sclerotization***: Mesothoracic furca hardly developed. Dorsum sclerotized, with weakly developed sclerotic cross bars and scleroits at bases of setae. ***Genitalia*** (Fig. 9C) in general appearance very similar to *S.* (*S.*) *quercus* with longer basal part of phallus.

Material examined. 1♂, 1♀ HUNGARY, Kisradoc, 29.ix.2011, *Quercus petraea*, Depa leg., coll. UŚ no. S 108; 4♀ POLAND, Świerklaniec, 2.xi.2010, *Q. robur*, Depa leg., coll. UŚ no. 2/12 A 1, 2, 3, 4; 2♂ SLOVAKIA, Svaty Jur, 3.x.2011, *Q. robur*, Depa leg., coll. UŚ no. S 137; 5♂ SLOVAKIA, Svaty Jur, 3.x.2011, *Q. robur*, Depa leg., coll. UŚ no. S 134, S 137.

Stomaphis (*Parastomaphis*) *graffii* Cholodkovsky, 1894

Lachnus longirostris Passerini, 1863
Stomaphis graffii acerinus Mamontova, 1963
Stomaphis acerinus Mamontova, 2012

Redescription, oviparous female (Figs. 1E,F, 6A, 15B; Table 1). ***Colour*** of live specimens: whitish, covered with wax powder. Mounted specimens: light brown. Head and legs dark brown, whole antennae little brighter. Legs brown, hind femora uniformly brown, hind tibiae light brown with internal edges brighter, having small scleroits at setae bases. Hind tarsi brown. Siphuncular sclerites, genital plate and cauda dark brown. ***Antennae*** 0.27–0.36 × BL and 1.31–1.66 × HW. VIb 0.23–0.30 × VIa; other antennal ratios: VI/III 0.45–0.57, V/III 0.53–0.71, IV/III 0.41–0.60. VIb with 2–3 apical and 15–20 subapical setae. ANT III with 4–13 sec. rhin., ANT. IV with 4–9 sec. rhin., ANT. V with prim. rhin. only, ANT. VI with prim. rhin. and 4–6 acc. rhin. dispersed over the distal half of VIa. Prim. rhin. on ANT V and VI slightly oval with delicate sclerotic rim. ***Rostrum*** when extended about 1.28–1.41 × BL. ARS 0.84–0.96 × ANT III and 1.32–1.52 × HT II. Labrum with numerous setae at base and with 33–42 setae along its elongated part. HT II 1.31–1.47 × MT II. ***Sclerotization***: Mesonotum with only marginal sclerites. Abd. terg. membranous except for siphuncular sclerites and single, very small scleroits on abd. terg. VII. Siphuncular sclerite longer than wide, covered with fine setae.

Redescription, male (Figs. 1G,H, 6B, 9D, 10A, 11A,B, 12A,B, 14A–D, 15A,B; Table 2). ***Colour*** of live specimens: light to dark olive green. Mounted specimens: body light brown, with head, legs and antennae darker, genitalia brown. Compound eyes each with 4–8 facets. ***Antennae*** 0.48–0.60 × BL and 2.24–2.71 × HW. In some specimens ANT III and IV not fully separated (Fig. 11B) or ANT IV–VI not properly developed (Fig. 11A). VIb 0.22–0.32 × VIa; other antennal ratios: VI/III 0.53–0.70, V/III 0.58–0.76, IV/III 0.25–0.56. VIb with 2–3 apical and 12–16 subapical setae. Prim. rhin. on ANT VI surrounded by 3–5 small acc. rhin. ***Sclerotization***: Pronotum and mesonotum weakly sclerotised. Mesothoracic furca hardly developed. ***Genitalia*** (Figs. 1G,H, 9D) projections of parameres elongated (shorter than basal part of phallus) and smooth, covered with few short setae on apices. Paired of lobate parts of parameres with numerous long setae. Basal part of phallus long, lanceolate, strongly sclerotized and dark pigmented on inner

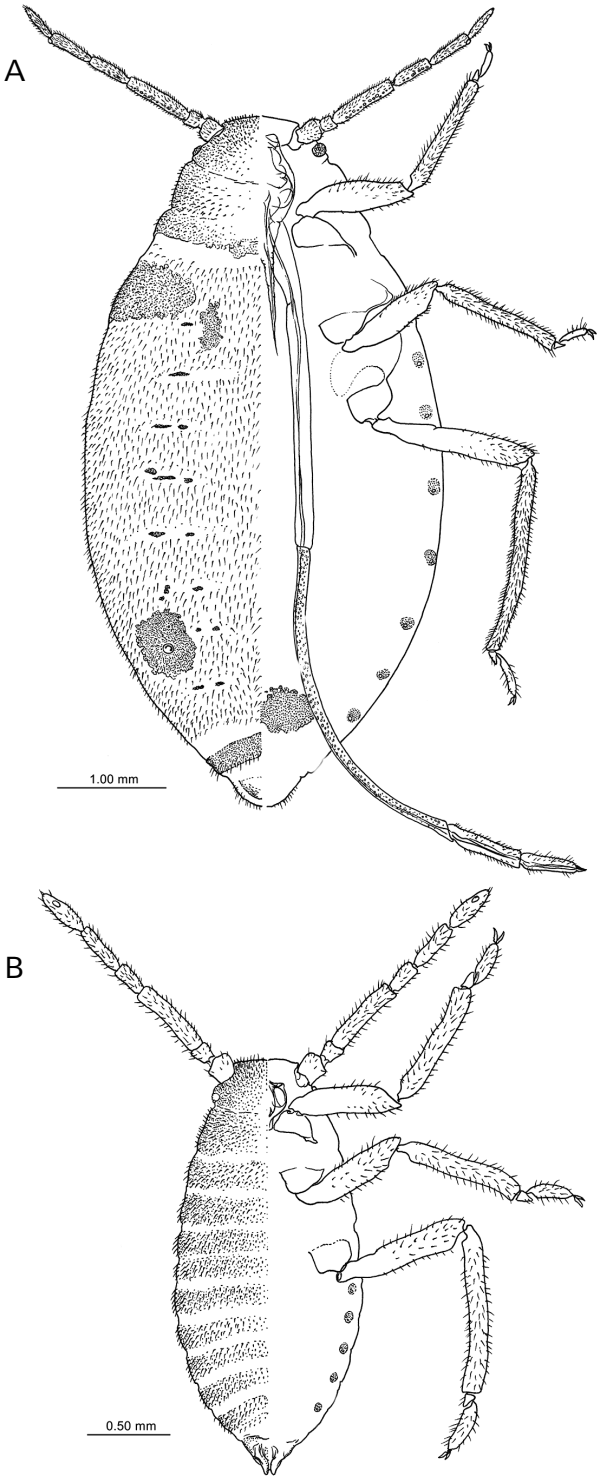

Fig. 6. *Stomaphis* (*P.*) *graffii*. **A**: Oviparous female. **B**: Male.

margin, with numerous long and erected setae distributed only on apices. Sclerotized arms of similar length to proximal and distal part, both robust and dark pigmented. First instar larva is characterized by presence of buds of parameres in form of small protuberances (Fig. 14A) whereas in second instar larva buds of parameres are elongated (Fig. 14C). In third instar larva also basal part of phallus with sclerotized arms is present (Fig. 14D).

Material examined. 1♂ FRANCE, Eughein, 20.ix.1968, *Acer* sp., Rabasse leg., coll. MNHN no. 17563; 4♂, 5♀ POLAND, Kalinowice, 2.x.2010, *A. platanoides*, Depa leg., coll. UŚ no. 10/10/2/12a; 3♂, 3♀ AUSTRIA, Neudorfl, 2.x.2011, *A. campestre*, Depa leg., coll UŚ no. S 126; 5♂, 2♀ CZECH REPUBLIC, Butowice, 28.ix.2011, *A. pseudoplatanus*, Depa leg., coll UŚ no. S 101; 13♂ juv., 8♀ POLAND, Gorzów Śląski, 18.viii.2010, *A. pseudoplatanus*, Depa leg., coll. UŚ no. S 42.

Stomaphis (*Parastomaphis*) *juglandis* Petrović, 1998

Redescription, oviparous female (Fig. 7A; Table 1). ***Colour*** of live specimens: dark brown (Petrović 1998). Mounted specimens: body light brown, with darker sclerotisations. Head brown, whole antennae as dark as head, with only bases of ANT III brighter. Legs brown, hind femora uniformly brown, hind tibiae light brown with internal edges brighter, having small scleroits at setae bases. Hind tarsi brown. Siphuncular sclerites, genital plate and cauda brown. ***Antennae*** 0.35–0.36 × BL and 1.93–1.98 × HW. VIb 0.18–0.23 × VIa, with small protuberances at apex; other antennal ratios: VI/III 0.42–0.43, V/III 0.53–0.56, IV/III 0.42–0.44. VIb with 3 apical and 15–17 subapical setae. Length of antennal setae slightly less than ant. BD. ANT III with 13–15 sec. rhin., segm. IV with 6 sec. rhin., segm. V with prim. rhin. only, segm. VI with prim. rhin. and 3–6 acc. rhin. dispersed over the distal part of VIa. Prim. rhin. on ANT V and VI slightly oval with delicate sclerotic rim. ***Rostrum*** when extended 1.59 × BL. ARS 0.77 × ANT III and 1.6 × HT II. Labrum with numerous setae at base and with 8 setae along its elongated part. HT II 1.45 × MT II. ***Sclerotization***: Mesonotum with only marginal sclerites. Mesothoracic and metathoracic furca separated, developed only as very short, blunt processes. Abd. terg. without sclerites except for siphuncular sclerites and a few very small scleroits at bases of setae on abd. terg. VII. Siphuncular sclerite longer than wide, covered with fine setae.

Redescription, male (Figs. 7B, 9E, 11F; Table 2). ***Colour*** of live specimens: dark green (Petrović 1998). Mounted specimens: body light brown, with head, legs and antennae darker, genitalia brown. Compound eyes each with about 8 facets. ***Antennae*** 0.54 × BL and 2.41 × HW. ANT V and VI not fully separated (Fig. 11F). VIb about 0.20 × VIa; other antennal ratios: VI/III 0.36, V/III 0.55, IV/III 0.37. VIb with 2 apical and 11–12 subapical setae. Prim. rhin. on ANT VI surrounded by 4–5 small acc. rhin. ***Sclerotization***: Pronotum and mesonotum weakly sclerotised. ***Genitalia*** (Fig. 9E) in general appearance similar to *S.* (*P.*) *graffii* with projections of parameres finger-like and almost hairless. Basal part of phallus dark pigmented on whole length.

Material examined. ***Paratypes***: 1♂ YUGOSLAVIA, Ilinci-Šid, 23.x.1996, İerinić leg., coll. MNHN no. 1765; 1♀ YUGOSLAVIA, Ilinci-Šid, 23.x.1996, İerinić leg., coll. MNHN no. 1766.

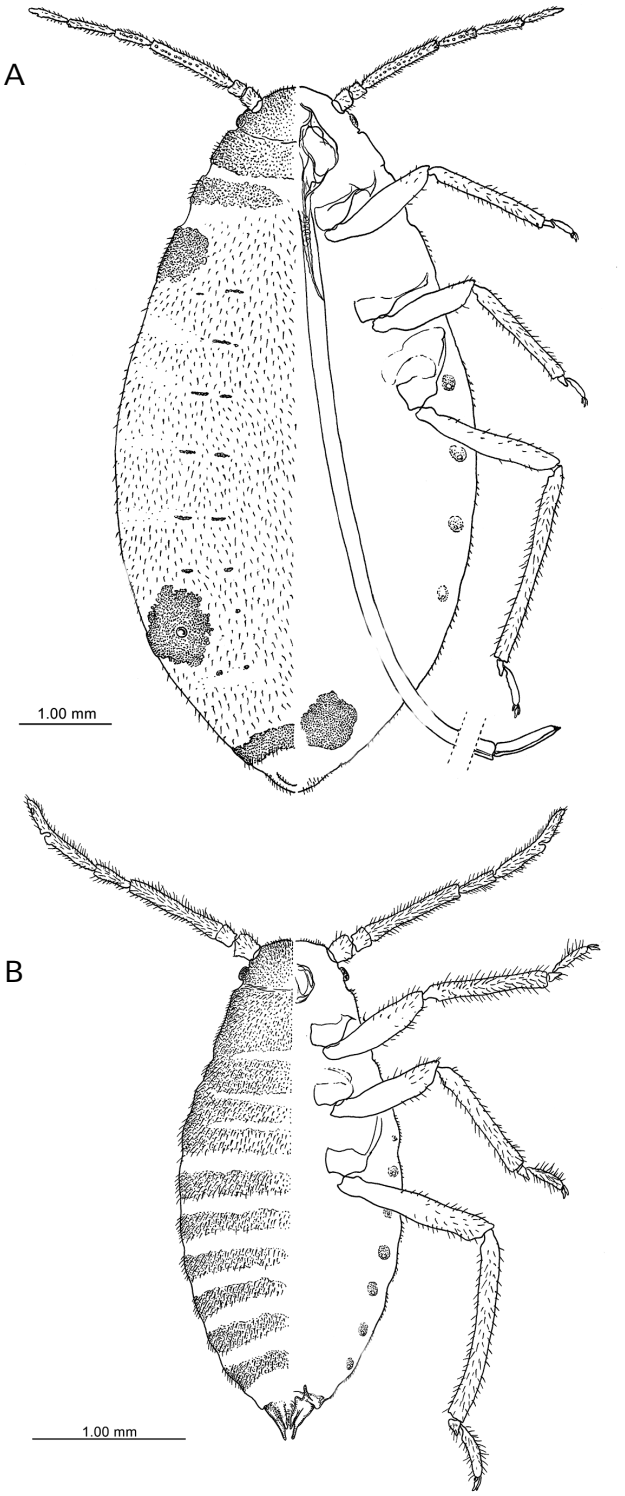

Fig. 7. *Stomaphis* (*P.*) *juglandis*. **A**: Oviparous female. **B**: Male.

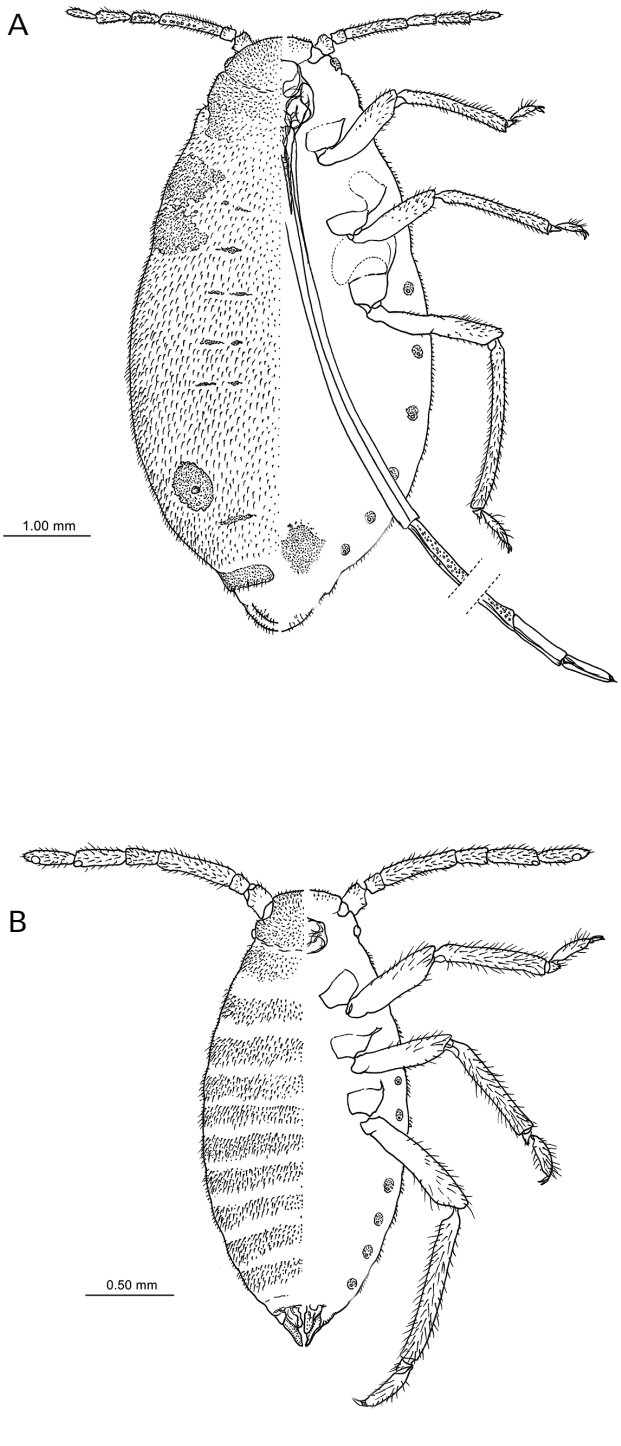

Fig. 8. *Stomaphis* (*P.*) *longirostris*. **A**: Oviparous female. **B**: Male.

Stomaphis (*Parastomaphis*) *longirostris*
(Fabricius, 1787)

Stomaphis bobretzkyi Mordvilko, 1901

Redescription, oviparous female (Fig. 8A; Table 1). ***Colour*** of live specimens: light brown or white when covered with wax powder. Mounted specimens: light brown, with darker sclerotisations. Head dark brown, whole antennae little brighter. Legs brown, hind femora uniformly brown, hind tibiae light brown with internal edges brighter, having small scleroits at setae bases. Hind tarsi brown. Siphuncular sclerites, genital plate and cauda dark brown. ***Antennae*** 0.28 – 0.32 × BL and 1.46 – 1.69 × HW. VIb 0.15 – 0.28 × VIa; other antennal ratios: VI/III 0.44 – 0.55, V/III 0.51 – 0.65, IV/III 0.43 – 0.58. VIb with 3 apical and 15 – 20 subapical se-

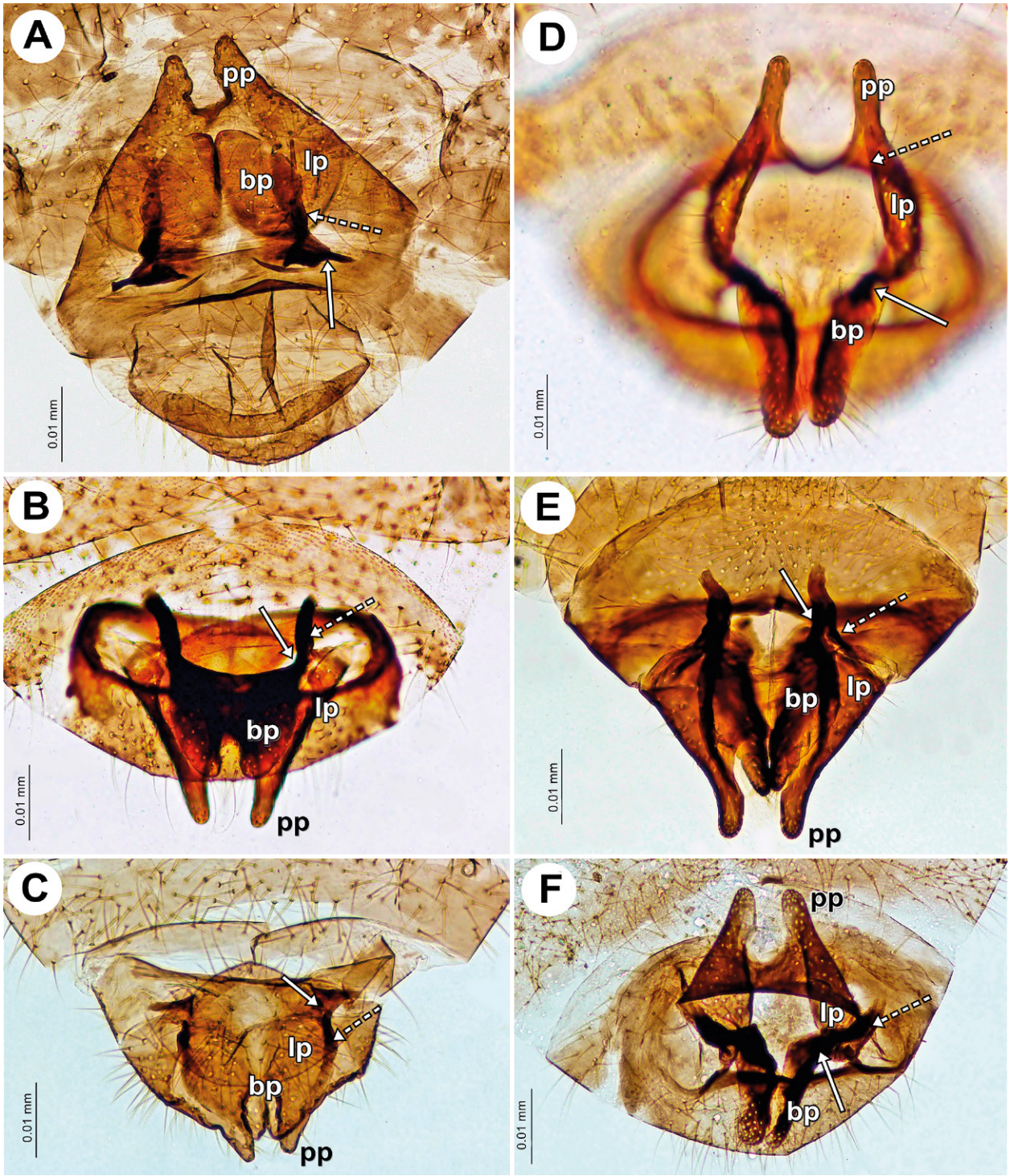

Fig. 9. External male genitalia of European *Stomaphis*. **A**: *S.* (*S.*) *quercus*. **B**: *S.* (*S.*) *radicicola*. **C**: *S.* (*S.*) *wojciechowskii*. **D**: *S.* (*P.*) *graffii*. **E**: *S.* (*P.*) *juglandis*. **F**: *S.* (*P.*) *longirostris*. — ***Abbreviations***: **bp** = basal part of phallus with sclerotized arms consists of short proximal (solid arrow) and long distal (dotted arrow) part, **lp** = lobate part of parameres, **pp** = projections of parameres.

tae. ANT III with 5–16 sec. rhin., segm. IV with 5–13 sec. rhin., segm. V with prim. rhin. only, segm. VI with prim. rhin. and 2–6 acc. rhin. dispersed over the distal part of VIa. ***Rostrum*** when extended about 1.34–1.65 × BL. ARS 0.90–1.05 × ANT III and 1.31–1.46 × HT II. Labrum with numerous setae at base and with 19–36 setae along its elongated part. HT II 1.34–1.55 × MT II.

Sclerotization: Mesonotum with only marginal sclerites. Abd. terg. membranous except for siphuncular sclerites and small sclerotic plates on abd. terg. VII. Some specimens show slight traces of glabrous sclerotisations in shape of longitudinal patches placed medially on abd. stern. II–IV. Siphuncular sclerite longer than wide, covered with fine setae.

Description, male (Figs. 8B, 9F, 11C,D; Table 2). ***Colour*** of live specimens: light to dark olive green. Mounted specimens: body light brown, with head, legs and antennae darker, genitalia brown. Compound eyes each with 2–6 facets. ***Antennae*** 0.45–0.64 × BL and 2.18–2.69 × HW. ANT III and IV (Fig. 11C) as well as V and VI (Fig. 11D) not fully separated in some specimens. VIb 0.17–0.29 × VIa; other antennal ratios: VI/III 0.48–0.74, V/III 0.56–0.83, IV/III 0.29–0.45. VIb with 2–3 apical and 11–16 subapical setae. Prim. rhin. on ANT VI surrounded by 1–5 small acc. rhin. ***Sclerotization***: Pronotum and mesonotum weakly sclerotised. ***Genitalia*** (Fig. 9F) in general appearance similar to above mentioned species of *Parastomaphis* with projections of parameres much shorter and covered with numerous setae.

Material examined. 2♂, 3♀ SLOVAKIA, Svaty Jur, 3.x.2011, *Populus nigra*, Depa leg., coll. UŚ no. S 135; 6♂, 8♀ CZECH REPUBLIC, Butowice, 28.ix.2011, *Salix alba*, Depa leg., coll. UŚ no. S 102; 1♂ FRANCE, Toulouse, 16.xi.1949, *Salix* sp., Lagarrigue leg., coll. MNHN 17567; 5♂, 4♀ AUSTRIA, Schrems bei Frohnleitn, 2.x.2011, *S. alba*, Depa leg., coll. UŚ S 124.

3.2. Aberrations of male morphology

Detailed analysis of the studied material revealed a very high portion (32%) of adult male specimens showing various morphological aberrations. The most striking examples were:

– apart from normally absent mouthparts, some individuals retained a residual rostrum, consisting either of apical rostral segment (ARS, segments IV + V) or of extremely shortened rostral segment III and ARS, with segments I and II always absent (Fig. 10);

– not fully separated antennomeres III and IV or V and VI, or even presence of unidentifiable and not developed segments separated from antennomere III (Fig. 11);

– not fully separated segments of legs e.g. undeveloped and not separated hind tarsus or not separated trochanter (Fig. 12).

Taking into account organs with aberrations, 12.00% of males had aberrant antennae, 17.33% had aberrant mouthparts and 2.67% had aberrant legs. The proportion of aberrant males varied across species, but this might be caused by an unequal number of studied specimens of particular species (Fig. 13). It is noteworthy that among the studied specimens, none had any aberrations in the genital apparatus.

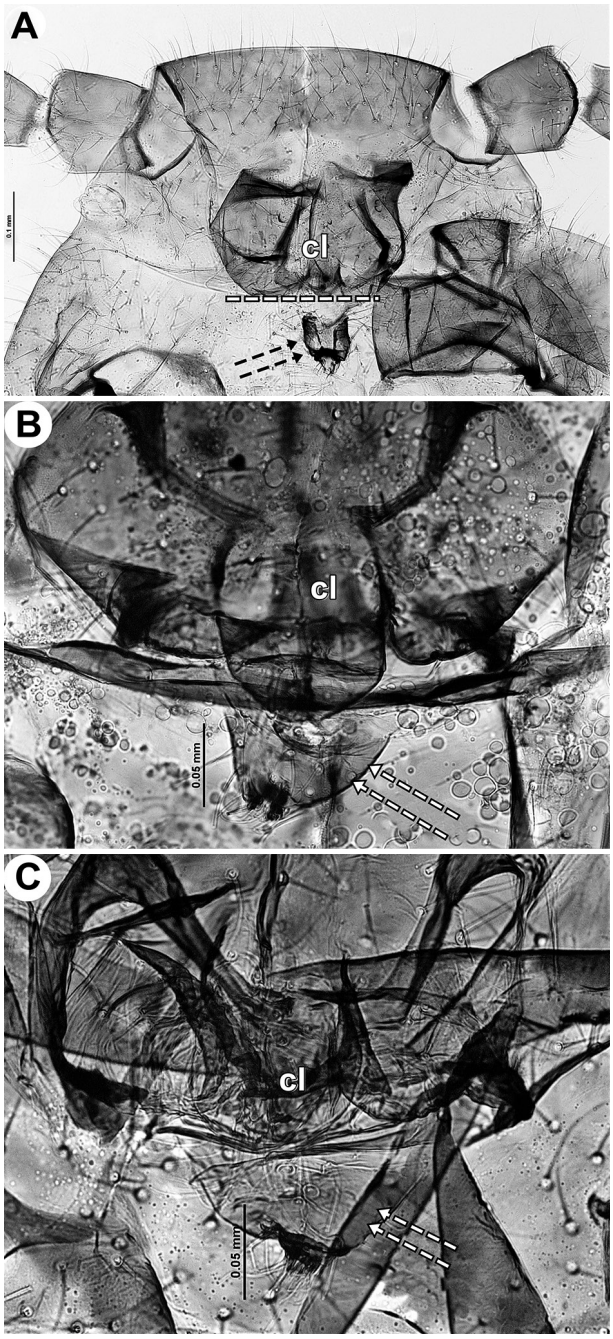

Fig. 10. Existence of residual mouthparts in males of European *Stomaphis* in form of apical segment of rostrum (double arrow) **A**: *S.* (*P.*) *graffii*. **B**,**C**: *S.* (*S*). *quercus*. — ***Abbreviation***: **cl** = clypeus.

3.3. Mating behavior

In Central Europe, where observations were conducted, sexuparae usually reach maturity in August. Oviparae and males appear in mid-August. Young males usually stay very close to their mother (Fig. 15A). After birth they are brightly yellowish and shining, but do not differ greatly in terms of size from the mature ones, except for the undeveloped genital apparatus and lack of sclerotization (Fig. 15B). They do not feed, as their mouthparts are reduced. The males of *S.* (*P.*) *graffii* molt three times, larval stadia I–III possess paired bundles of parameres whereas in the stadium III the sclerotized basal part of the phallus with its articulation additionally have been observed (Fig. 14).

After maturing, the mating behavior occurs. Living close to the other aphids of the colony, males do not undertake extensive searches for females, but in *S.* (*S.*) *quercus*

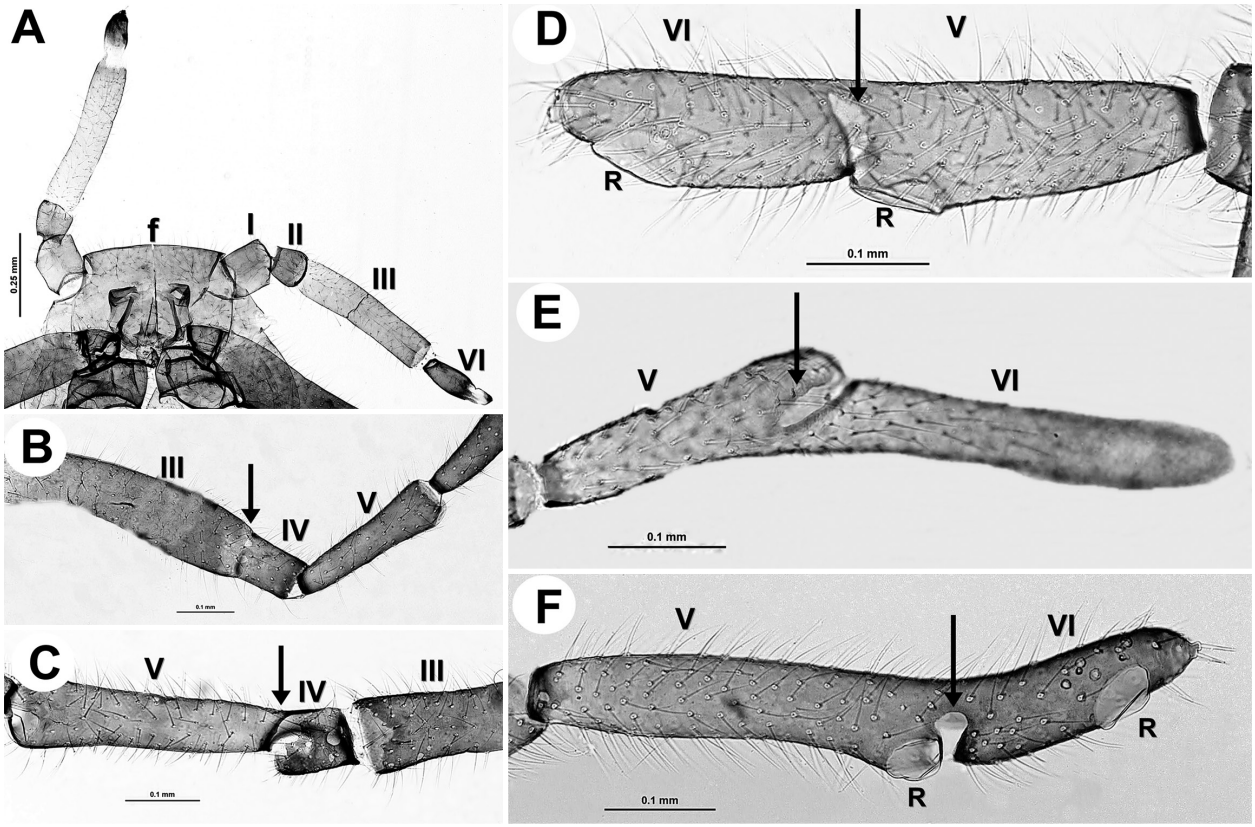

Fig. 11. Aberrations in male antenna morphology of European *Stomaphis*. **A**: Not properly developed segments of antennomeres IV–VI of *S.* (*P.*) *graffii*. **B**: Not fully separated antennomeres III and IV of *S.* (*P.*) *graffii*. **C**: Not fully separated antennomeres III and IV of *S.* (*P.*) *longirostris*. **D**: Not fully separated antennomeres V and VI of *S.* (*P.*) *longirostris*. **E**: Not fully separated antennomeres V and VI of *S.* (*S.*) *radicicola*. **F**: Not fully separated antennomeres V and VI of *S.* (*P.*) *juglandis*. — ***Abbreviations***: **f** = frons, **R** = rhinarium, **I–VI** = antennomere I–VI.

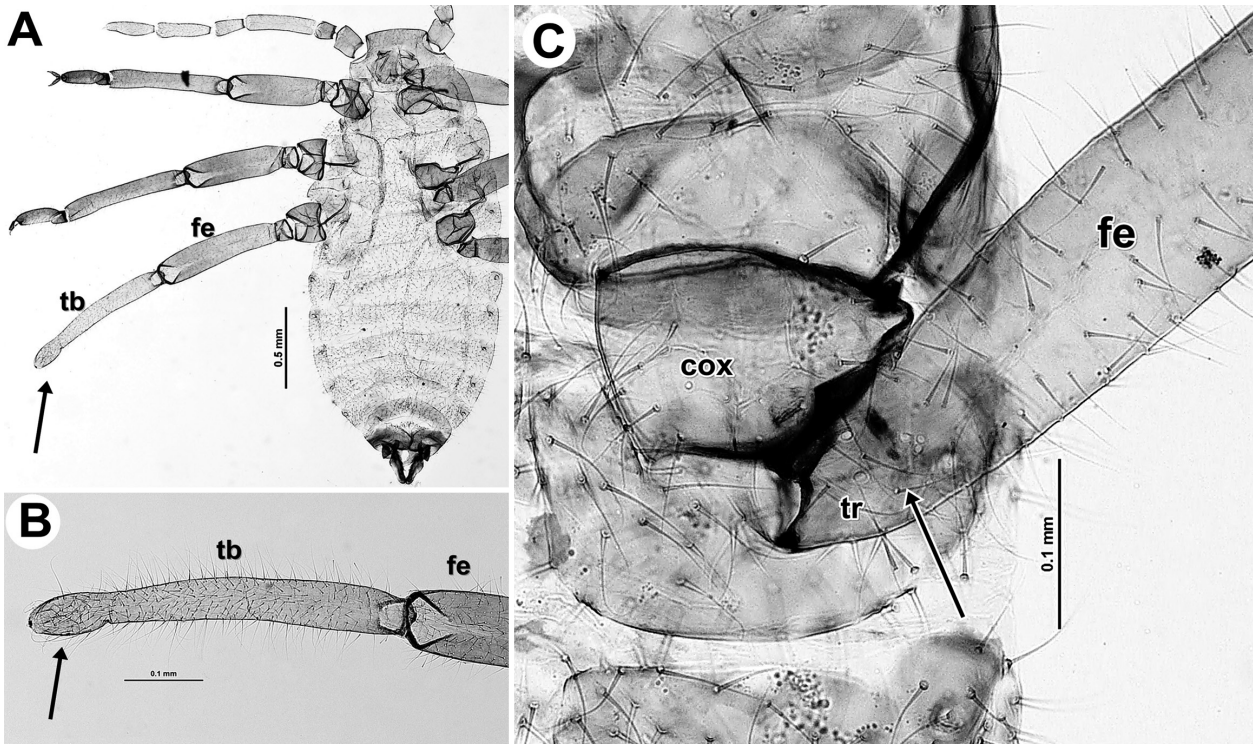

Fig. 12. Abberations in male leg morphology of European *Stomaphis*. **A**,**B**: Not properly developed hind tarsus (arrow) of *S.* (*P.*) *graffii*. **C**: Lack of separation of hind trochanter and femur, arrow indicates the absence of trochantro-femoral suture of *S.* (*S.*) *wojciechowskii*. — ***Abbreviations***: **fe** = femur, **tb** = tibia, **cox** = coxa, **tr** = trochanter.

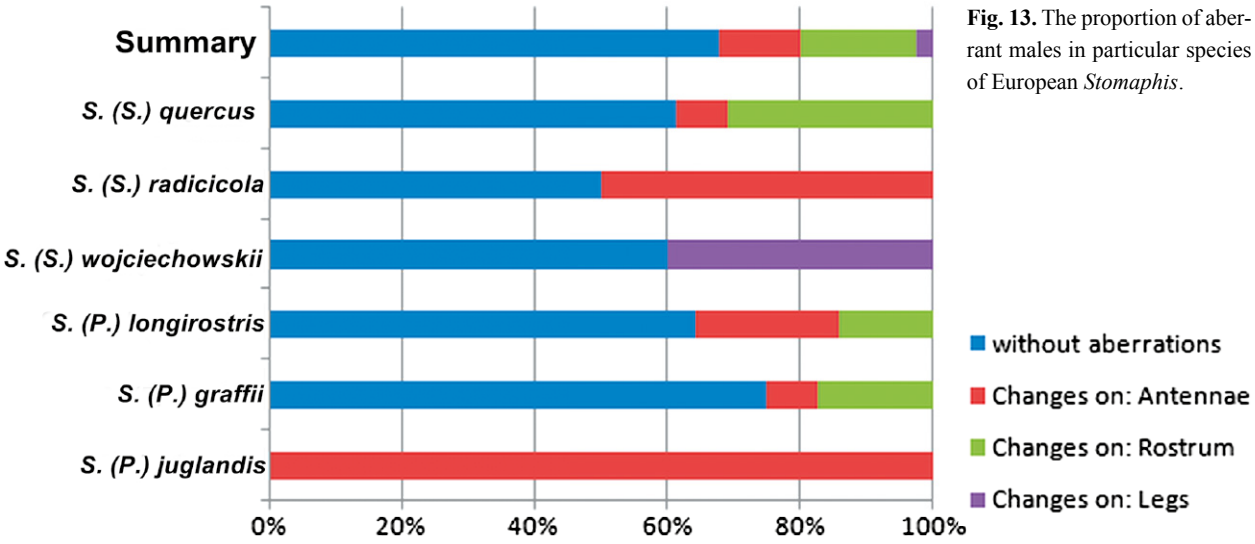

Fig. 13. The proportion of aberrant males in particular species of European *Stomaphis*.

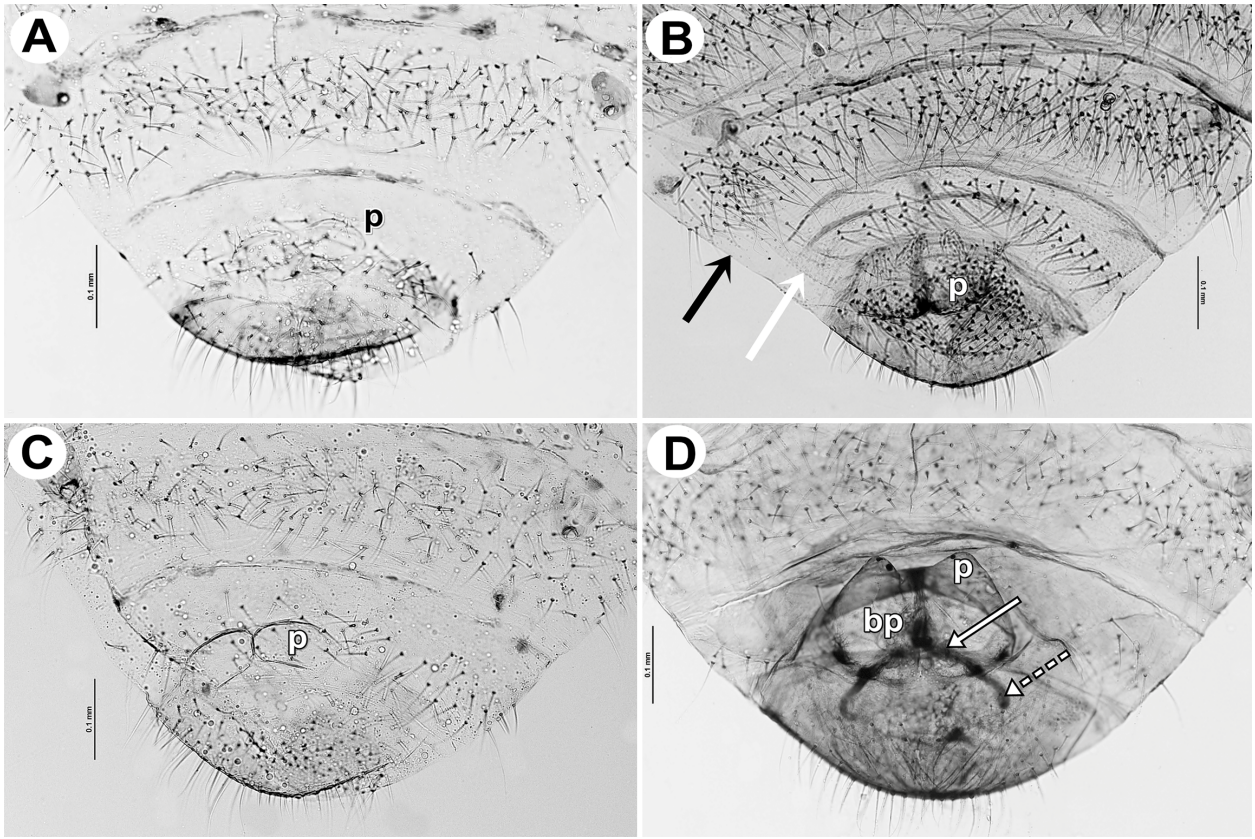

Fig. 14. Development of external male genitalia on the example of *S.* (*P.*) *graffii*. **A**: First instar larva with buds of parameres in form of small protuberances. **B**: First instar larva (black arrow) in the moment before molting. White arrow indicates the second instar larva. **C**: Second instar larva with elongated buds of parameres. **D**: Third instar larva. — ***Abbreviations***: **p** = paramere buds, **bp** = basal part of phallus buds with sclerotized arms consists of short proximal (solid arrow) and long distal (dotted arrow) part.

some males have been observed to move in search for females. Very often several males keep close to an oviparous female, to such an extent that they climb onto her dorsum. It is not known whether one female copulates with more than one male, however, several adult males sitting on a single oviparous female have been observed (Fig. 15C). It is thus probable that a series of copulations may take place. A very interesting departure from the typical mating position of a male has been observed in *S.* (*P.*) *longirostris* and *S.* (*P.*) *graffii*, where the male takes a position beneath the female (ventro-ventral) during copulation and usually is completely hidden under the abdomen of the oviparous female (cryptic sex). It is suspected that this peculiarity might have developed as a

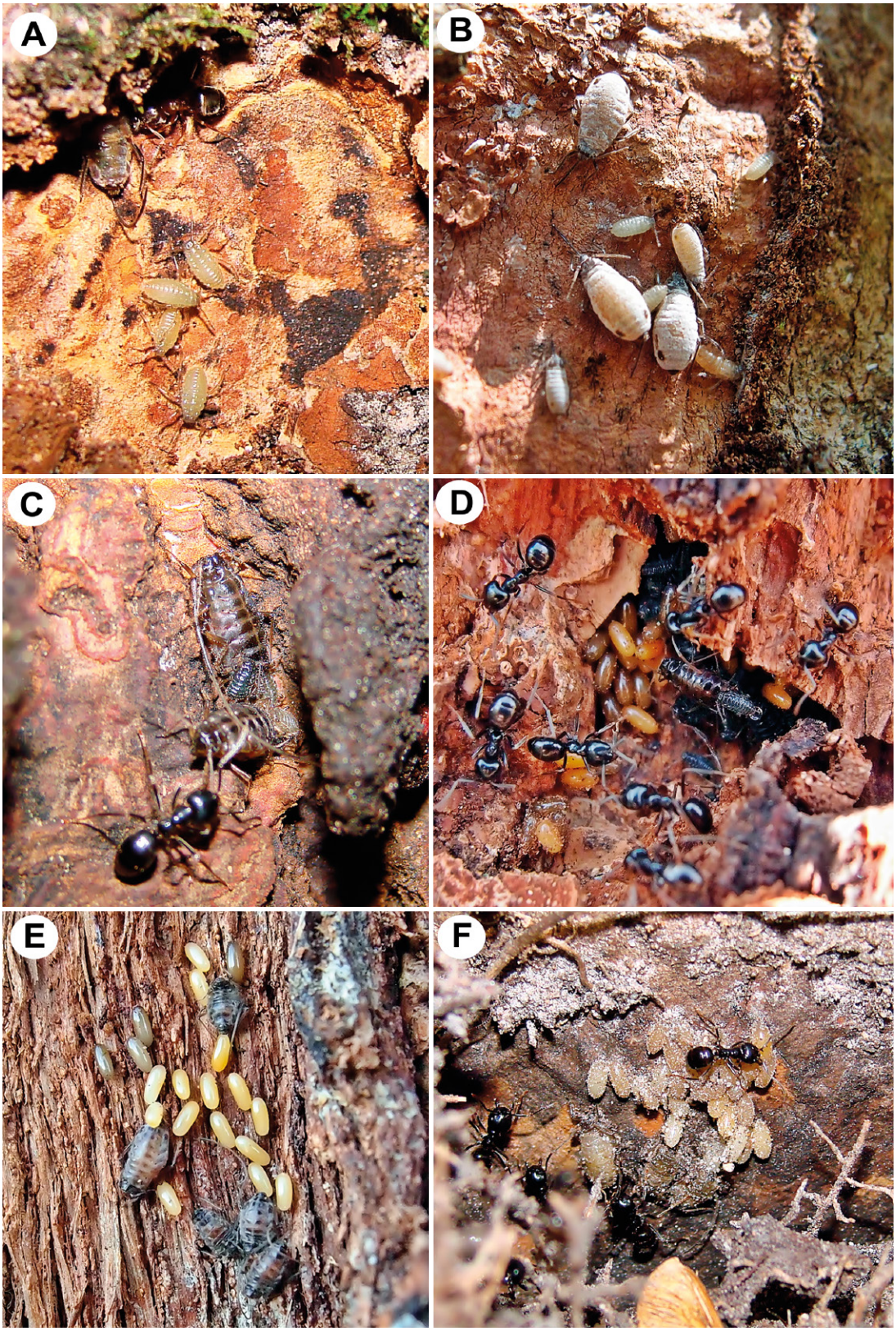

Fig. 15. Mating behavior of European *Stomaphis*. **A**: Freshly born males of *S* (*P.*) *graffii* on *Acer pseudoplatanus* aggregated in ant chamber under the bark; above their mother – sexupara, attended by the ant *Lasius brunneus*. **B**: Feeding oviparous females (3 adults and 3 larvae) accompanied by second instar larvae of males of *S.* (*P.*) *graffii*. **C**: Dorso-ventral copulation of *S.* (*S.*) *quercus* on *Betula pendula* attended by *L. fuliginosus*; visible rostrum of female moved aside during copulation; recently moulted male copulates during the presence of the second male also sitting on the abdomen of female. **D**: Dorso-ventral copulation of *S.* (*S.*) *quercus* on *Quercus robur*; visible droplet of honeydew, excreted by copulating female; clusters of eggs laid in the crevices of bark. **E**: Oviparous females of *S.* (S.) *wojciechowskii* on *Q. robur* with clusters of laid eggs. **F**: Oviparous females of *S.* (*P.*) *graffii* and clusters of eggs laid at the base of trunk of *A. pseudoplatanus*, in ant chamber under the soil level; visible worker of *L. fuliginosus* attending the cluster of eggs.

form of mate guarding behavior or avoidance of competition with other males. During the copulation, the female either moves the rostrum aside, beyond the legs (*S.* (*S.*) *quercus*) or it is feeding (*S.* (*P.*) *graffii*), so in both cases the very long rostrum does not disturb the copulation.

After the copulation the oviposition starts. A female lays approximately 4–7 eggs, usually in clusters, either in deep bark crevices, if it belongs to the species that lives on the surface of the trunk (*S.* (*S.*) *quercus* Fig. 15D), or in the ant chambers built under the bark (*S.* (*P.*) *graffii*, *S.* (*P.*) *longirostris*), or in the cork tissue of the tree (*S.* (*S.*) *wojciechowskii* Fig. 15E). Sometimes big clusters of eggs have been recorded at the base of the trunk, inside the nest of ants (Fig. 15F) which take care of them. The eggs are yellowish just after the oviposition, and get darker during the consecutive days, to become dark greenish or brownish.

4. Discussion

4.1. Taxonomic status of "*Parastomaphis*"

On the basis of the structure of the apical part of antennomere VI (rounded apex in *Stomaphis* and nodulose apex in *Parastomaphis*) of the viviparous generation, Pašek (1953) subdivided the genus *Stomaphis* into two subgenera: *Stomaphis* Walker and *Parastomaphis*, later treated as separate genera (Szelegiewicz 1978). Then *Parastomaphis* was synonymized with *Stomaphis* by Remaudière (1997) and current aphid taxonomy retains this taxon undivided as a single genus within the tribe Lachnini (Nieto Nafria & Favret 2011).

In the sexual generation there are even more significant and meaningful features distinguishing the two subgenera than those mentioned by Pašek. The most important is the division of the genital plate into two separate subplates – characteristic for *Parastompahis* contrary to the undivided genital plate in *Stomaphis* – as it has a direct correlation with the observed ecological difference in the mode of copulation in this subgenus, i.e. the cryptic sex. The subdivided genital plate correlates with significantly longer parmeres of males of *Parastomaphis*, serving to strain both subplates of the female during ventro-ventral copulation, also a unique behavior not only among aphids but also among other insect taxa (Depa et al. 2014). Moreover, in the sexual generation of the subgenus *Parastomaphis*, similarly to the viviparous generation, apical setae on the processus terminalis arising from nodulose bases and setae in males, distributed over the antennae and legs, are much shorter than in the representatives of the subgenus *Stomaphis*.

Our analysis of morphological features of the sexual generation of the European representatives of this genus, supported by biological data, leads to the conclusion that Pašek's (1953) proposition of a separate subgenus *Parastomaphis* should be maintained. In general, morphological features of viviparous females (fundatrices and fundatrigeniae) are repeated in oviparous females. Ventral plates are present in subgenus *Stomaphis*, which seems to be an apomorphic character, since no other Lachninae possess ventral plates, versus their absence in subgenus *Parastomaphis* (Depa & Mróz 2012; Depa & Kanturski 2014). Moreover, long rostrum, much longer than body, is a synapomorphy of all species of the genus *Stomaphis*, not observed in any other representative of Lachninae.

4.2. Reproductive strategy – guarding or active searching?

In aphids, as in many other insect groups, male genitalia are highly complex, integrated suites of morphological structures whose function often remains obscure. As expected, comparative evidence shows that the genitalia diversify much more rapidly in insect clades characterized by polyandrous mating systems than in taxa characterized by monandry (Cayetano et al. 2011). Among the Aphididae species studied so far, the lachnines are characterized by the most diverse male genitalia, especially in the structure of parameres (Wieczorek et al. 2012). The Lachninae, treated as a "basally positioned" lineage in the evolution of Aphididae (Ortiz-Rivas & Martinez-Torres 2010), differ from other aphids, as many species may infest the same host plant while being specialized for different feeding sites on the host plant, which plays a more important role in their speciation than host specificity (Favret & Voegtlin 2004). European representatives of the genus *Stomaphis* are associated mostly with deciduous trees, but are rarely recorded from the same host plant (Blackman & Eastop 2014). Exceptions include *S.* (*S.*) *quercus* and *S.* (*S.*) *wojciechowskii*, sharing *Quercus* spp. as a host plant while occupying distinct ecological niches on it – bark crevices on trunk versus basal part of trunk in ant shelters constructed within bark crevices and covered by soil (Depa et al. 2012). In this way, the differentiation of the male genitalia, mostly the length and shape of parameres, is more important during copulation than in the species-specific selection. It corroborates our observation of two types of copulation in the subgenera *Stomaphis* and *Parastomaphis*: dorso-ventral or ventro-ventral respectively. The East Palaearctic representatives of the genus *Stomaphis* are characterized by even more diverse parameres than European ones (Sorin 1995, 2012; Wieczorek et al. 2012), however, their mating behavior has not been reported. Generally, relatively little is known about copulatory behavior of aphids (Foster & Benton 1992; Kozłowski 1991; Dagg 2002, 2003; Dagg & Scheurer 1998; Depa et al. 2014), but species with more female-biased sex ratios are not expected to show guarding behavior, whereas species with less female-biased sex ratios are expected to show guarding behavior or copulate for a longer time than is necessary for ferti-

lization (Dixon 1998). However, in case of *Stomaphis* it is very difficult to establish the male-female ratio, due to their very cryptic life mode. In *S. yanonis* Takahashi Takada (2008) and in *S. quercus* (L.) Loi et al. (2012) observed one to three males climbing onto the abdomen of one ovipara, which was similar to our observations. It is not known whether males compete for the female but it is possible, due to limited space in ant chambers, in the case of species having a cryptic mode of life. A similar guarding behavior was observed in other lachnid males (genera *Lachnus* Burmeister and *Cinara* Curtis), where additionally oviparous females were marked with pheromones from the males' hind tibiae and aedeagus (Dagg & Scheurer 1998). Males of lachnids cannot retract their aedeagus into the abdomen (Dagg 2002), whereas males of other aphid taxa retract their aedeagus into the abdomen immediately after copulation and often do not feature the striking postcopulatory courtship (e.g. *Myzus persicae* (Sulzer) Doherty & Hales 2002; *Uroleucon cirsii* (L.) Dagg 2002). The studied species of the genus *Stomaphis* also have an enormous aedeagus, still not retracted after copulation, and probably they also mark oviparous females.

4.3. Hypothesis of evolution of male dwarfism in *Stomaphis*

The most striking feature of the genus *Stomaphis* as a whole is the strong sexual dimorphism, the extent of which varies among aphids. In some cases males are winged and do not differ significantly from winged viviparous females (e.g. *Lachnus roboris* (L.) – Wieczorek et al. 2012). In some cases males can be wingless, but do not differ in size from oviparous females (e.g. *Lachnus pallipes* (Hartig) or *Pterochloroides persicae* (Cholodkovsky) – Wieczorek et al. 2012, 2013). Sometimes both males and oviparous females are small and dwarfish, but still able to feed (e.g. *Anoecia corni* (Fabricius) – Wieczorek 2008) or remain arostrate (Eriosomatinae).

The case of sexual generation in the genus *Stomaphis* is significant due to the large body size of females and the reduced size and morphology of males. This is a typical case of so-called dwarfish males, where the body length of males does not exceed 50% of the length of oviparous females (Table 3), corresponding to a much higher disparity in body volume (ca. 12%). Such a score well matches the proportion typical for dwarfish males in other animals (Ricci & Melone 1998).

There are various explanations for the existence of dwarfish males. According to a general concept, both a sedentary life mode of females and a lack of competitive behavior among males can promote male dwarfism (Vollrath 1998). Moreover, in *Stomaphis* we observe a significant amount of various aberrations of male morphology. However, the presence of an aberrant, residual and non-functional rostrum (lack of stylets) in some male specimens (in ca. 17.33% of males) indicates the earlier evolutionary condition when mouthparts were well-developed and certainly functional. The presence of such an aberrant, residual condition, plesiomorphic in its nature, indicates that the process of morpho-reduction of mouthparts took place quite recently in the evolutionary history of *Stomaphis*. It should not be surprising, taking into account that this is a relatively young genus, with the only known fossils coming from the Middle Miocene (ca. 15 mya) – *S. eupetes* Mamontova & Wegierek (Wegierek & Mamontova 1993). Furthermore, lack of any residual wings may indicate that the loss of wings preceded the reduction of mouthparts. On the other hand, further morphological changes, including not fully separated antennomeres, coxae and trochanters, indicate an ongoing process of further reduction of male body parts. It is possible that these aberrations could be caused by the lack of feeding across multiple molts, however, there was not enough nymph specimens for detailed analysis.

Table 3. Proportion of the size of males versus oviparous females of the European species of the genus *Stomaphis*.

	male length / female length
Stomaphis (*Stomaphis*) *bratislavensis*	53.96%
Stomaphis (*Parastomaphis*) *juglandis*	44.98%
Stomaphis (*Stomaphis*) *radicicola*	44.38%
Stomaphis (*Parastomaphis*) *graffii*	44.00%
Stomaphis (*Parastomaphis*) *longirostris*	40.89%
Stomaphis (*Stomaphis*) *quercus*	39.43%
Stomaphis (*Stomaphis*) *wojciechowskii*	37.98%

In our opinion we can observe two phenomena: dwarfism, as a reduction of body size and reduction of various morphological structures, which might also be considered as a part of process of dwarfing. When considering the reasons for these phenomena a series of possible factors should be taken into account:

(1) Size. As a part of adaptation to feeding on tree trunks, females of the genus *Stomaphis* developed extremely long mouthparts, which enabled them to probe through the thick cork tissue of trees. This morphological adaptation to feeding on tree trunks is a phenomenon well documented even in fossil aphids, both in fossil *S. eupetes* as well as in older and unrelated, extinct aphid taxa (Wegierek & Grimaldi 2010; Homan & Wegierek 2011). This has led to an increase of their size to the limits unseen in other aphid genera, according to the tendency of correlating the body size with the size of mouthparts, depending on the feeding location (Dixon 1998). However, the enlarged size of the mouthparts leads to difficulties with escape behavior when in danger. Therefore, either finding an appropriate shelter or some sort of mutualistic partners providing protection against predators is required.

(2) Mutualism with ants. Finding a mutualistic partner was a necessary part of adaptation to feeding on tree trunks by *Stomaphis*. All known species belonging to this genus are obligate myrmecophilous and cannot survive without ant attendance (Lorenz & Scheurer 1998;

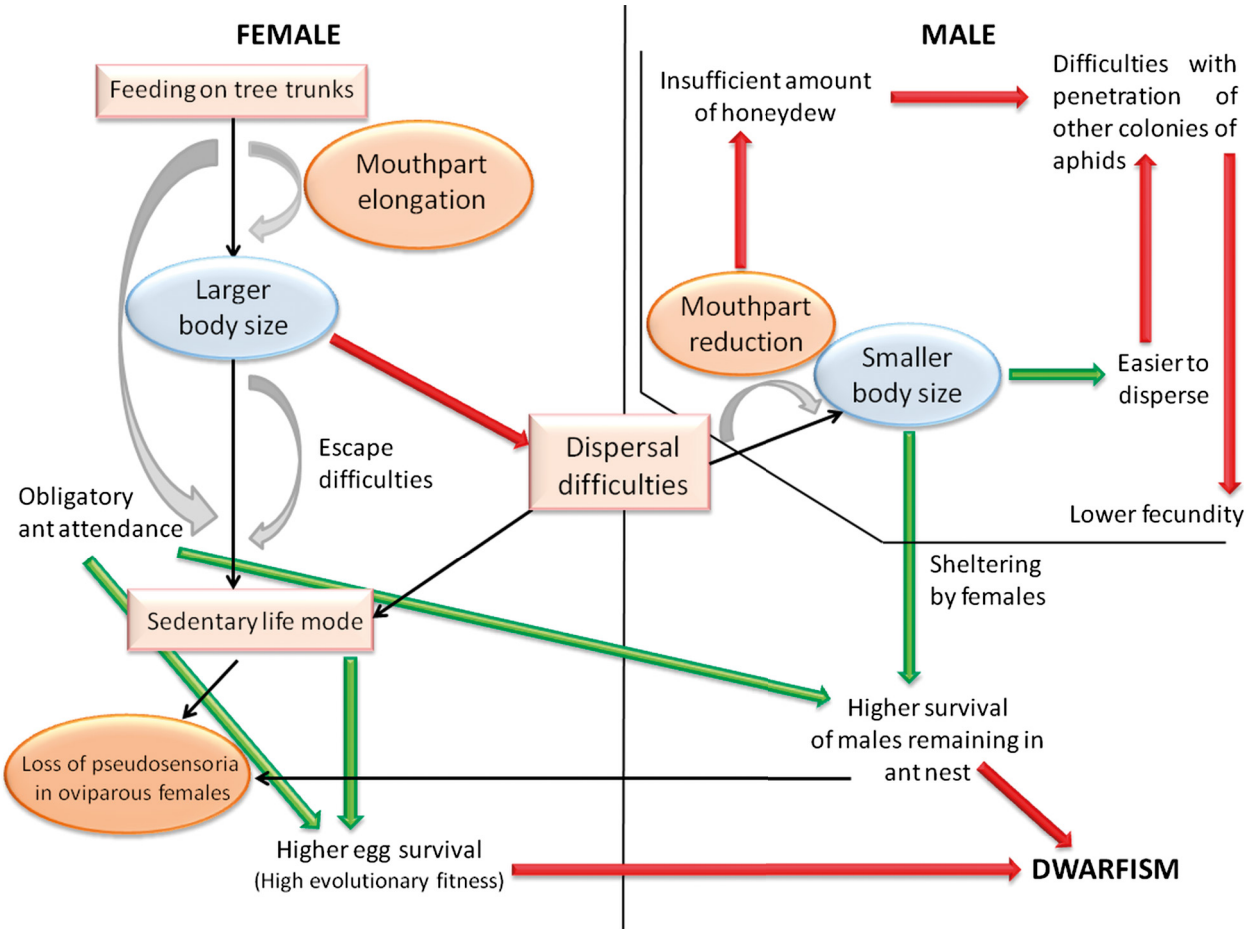

Fig. 16. The probable course of development of male dwarfism in the genus *Stomaphis*. **Boxes** = ecological traits, **blue ellipses** = morphological traits, **orange elipses** = morphological processes; **green arrows** = favorable changes, **red arrows** = unfavorable changes.

Matsuura & Yashiro 2006). Ants, providing shelter and protection from enemies, allowed aphids to broaden their ecological niche to underground parts of trees, very deep bark crevices covered by soil and even ant chambers built inside cork tissue (Loi et al. 2012).

(3) Dispersal abilities. Species of this genus rarely feed on younger trees. They usually feed on older trees, with thicker bark, where ants can build their tunnels in bark crevices at the base of the trunk as well as under the soil, or finally build their chambers in the bark (Depa et al. 2012). This has led to limiting the movement possibilities of these aphids either inside ant nests or outside. Moreover, apart from big size and poor flight abilities (Takada 2008) they also depend on the presence and quick finding of an appropriate ant species.

The above mentioned factors (1)–(3) resulted in two successive phenomena strictly connected with the process of male dwarfing (Fig. 16): The first phenomenon is a sedentary life mode of females, which significantly increased the necessity of active searching for females by males during the mating period. Being the first step of the process leading to male dwarfism, it could rely on decreasing the sizes of males by reducing feeding, in order to promote dispersal abilities, through the lower mass of body (see also the "gravity hypothesis" of male dwarfism by Moya-Laraño et al. 2002). If females left the ant nest, they had to find a new nest after mating, to increase the chances of fundatrices survival in spring. Thus, the promoted strategy was not to leave the ant nest and wait to be found by males instead. We do not share Dixon et al.'s (1998) point of view that the mouthpart reduction in males of *Stomaphis* is an adaptation allowing for mating, since the long rostrum would disturb copulation. As observed in many species of *Stomaphis*, the female may change the position of the rostrum during copulation, and we believe that the male could potentially do the same (Depa et al. 2014). If the reduction of mouthparts and body size promoted a more effective dispersal of males, by decreasing their body weight, it simultaneously decreased their attractiveness to ants, as their honeydew production was significantly diminished or even stopped. And that certainly influenced their ability to penetrate the ant nest in search for females, by increased aggressiveness and predatory behavior of ants towards males.

As a result of the sedentary life mode of females, simultaneously with the morphological reductions, the second phenomenon took place: the co-occurrence of males and females within the same ant nests, with no possibility of an escape for females. This resulted in their copulation within the ant nest with males that did not un-

dertake the search for a mate. This probably increased competition among males and might have influenced the development of the ventro-ventral copulation type in the subgenus *Parastomaphis* (Depa et al. 2014). Local mate competition was also observed in *Uroleucon cirsii* (Dagg & Vidal 2004), however this species copulate in dorso-ventral position, typical for other aphids.

At some point the second way of reproduction – copulation with indoor males rather than with those arriving from other colonies – began to be promoted by natural selection, probably through a lower mortality of males. Females fertilized by the indoor males had a better reproductive success than the females which were not fertilized at all in the case when no male could get into the ant nest. The limited competition among males within the colony promoted the tendencies involving the decreasing body size and further reduction of mouthparts. The safe environment of the ant nest led to the reduction of siphunculi. No need of active searching for females decreased the number of secondary rhinaria (as it happens e. g. in *Cinara* spp.: Eastop 1972). The same process led to the reduction of pseudosensoria on tibiae of oviparous females which did not need to attract males. Perhaps the presence of oviparous females simultaneously with still subadult males led to neoteny, by retaining the larval appearance and e.g. undeveloped wings, which were in fact not necessary. Similar tendencies may be observed also in the under-bark living beetles of the genus *Ozopemon* (Curculionidae) (Jordal et al. 2002).

As males of the genus *Stomaphis* are arostrate, consequently the retort-shaped organs, stylets, pharyngeal duct, pharyngeal valve, gustatory organs, salivary glands, and the salivary pump are not present in them (Ponsen 1997). The complicated filter system which is present in all investigated species of the Lachninae (Ponsen 1981) is absent from the degenerated midgut as well as the mycetome (Ponsen 2006). In this way, males are less attractive for ants, as they do not produce honeydew. This would partly explain their behavior of staying close to either their mothers after birth or climbing onto oviparous females before copulation. The presence of honeydew producing females could mask the presence of males or some influence of female pheromones may be a factor preventing ants from eating males. Aphids, especially larvae, are often treated as a source of proteins and eaten by ants that keep them in their nests (Pontin 1978).

This is only true if in the first stage of evolution of the common ancestor of *Stomaphis* both, alate and apterous males existed, as it happens for example, in the *Cinara cembrae* (Cholodkovsky), where single species has both alate and apterous males (Pintera 1966), or in not related species *Chaitophorus populeti* (Panzer), where both alate and apterous males occur (Wegierek 2000). In that situation, when mouthpart reduction co-occurred in both male morphs, apterous males remaining in colony had better chances of survival than dispersing alate males, which had higher mortality and lower fecundity.

This way, the developmental line of apterous males with reduced mouthparts was supported by selective factors (higher fecundity) and with sedentary life mode of large females, continues with further reduction of morphological structures.

The observed male dwarfism concurs well with the theories presented by Vollrath (1998). A considerable number of interdependent phenomena connected with feeding adaptations and relations with their mutualistic partners show the whole complexity of ecological factors influencing the development of male dwarfism in aphids, as presented in Fig. 16. Similar problems with clarification of influence of various factors leading to male dwarfism were encountered also in other groups of invertebrates e.g. spiders from the family Lycosidae (Logunov 2011) or in spionid polychaetes (Vortsepneva et al. 2008).

In the case of *Stomaphis*, we can observe not only dwarfism, but a high ratio of various aberrations, including a reduction of the number of antennomere. Interestingly, we do not find remnants of wings, but we can observe the remnants of mouthparts. This supports the thesis that apterous males could have represented the first stage of their dwarfing, and the loss of mouthparts has been more recent and contemporary to the development of the whole genus *Stomaphis*, as, unlike *Lachnus*, all species of this genus have dwarfish males. The next evolutionary step could be similar to that of *Trama* von Heyden (Blackman et al. 2001), with permanent parthenogenesis and only occasional occurrence of males, or of *Tuberolachnus salignus* (Gmelin), in which no sexual generation has ever been recorded.

In two of the European species of *Stomaphis* we observe permanent parthenogenesis. Both live in warm, Mediterranean climate (*S. acquerinoi* Binazzi – Italy, *S. cupressi* Pintera – Western and Eastern Mediterranean region) (Nieto Nafría et al. 2002; Binazzi & Pennacchio 2002). It is interesting, whether permanent elimination of males is the result of a warmer climate (as in the Lachninae *Pterochloroides persicae* – Wieczorek et al. 2013) or the result of ongoing reduction of male morphology. If the suspected high rate of inbreeding in *Stomaphis* does not disturb its ecological fitness, the total elimination of the sexual generation may have no influence on its survival. The anholocycle is frequent in the Lachninae (*Tuberolachnus* Mordvilko, *Pterochloroides* Mordvilko, *Trama*) so it may also refer to *Stomaphis*. It may be an intermediate stage between the condition where both winged and wingless males exist in various species belonging to a single genus (*Lachnus*) and the condition where males are reduced in size and appear sporadically (*Trama*) (Blackman et al. 2001), and may further lead to permanent parthenogenesis.

The presented hypothesis of the course of evolution of the male dwarfism in *Stomaphis* requires further investigations and needs to be supported by more evidence. The following questions need to be answered: **1.** What is the sex ratio in sexual generation of *Stomaphis*? **2.** What are the dispersal abilities of *Stomaphis* males? **3.** How ant workers treat males inside and outside the nest (with or without females)? **4.** What is the rate of inbreeding in *Stomaphis* (how often sib-mating occurs)? **5.** What is the

ratio of aberrant male nymphs among freshly born individuals?

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